Herbert W. Rand

TEXT-BOOKS OF ANIMAL BIOLOGY
Edited by JULIAN S. HUXLEY, M.A.
Fullerian Professor of Physiology, Royal Institution
Honorary Lecturer in Experimental Zoology, King's College, London

VERTEBRATE ZOOLOGY

VERTEBRATE ZOOLOGY

H.W.Rand

AN INTRODUCTION TO THE COMPARATIVE ANATOMY, EMBRYOLOGY, AND EVOLUTION OF CHORDATE ANIMALS

BY

G. R. DE BEER, M.A., B.Sc., F.L.S.

FELLOW OF MERTON COLLEGE, JOHN WILFRED JENKINSON MEMORIAL
LECTURER IN COMPARATIVE AND EXPERIMENTAL EMBRYOLOGY
IN THE UNIVERSITY OF OXFORD

WITH AN INTRODUCTION BY

JULIAN S. HUXLEY, M.A.

ULLERIAN PROFESSOR OF PHYSIOLOGY ROYAL INSTITUTION

NEW YORK

THE MACMILLAN COMPANY

1928

TO

KITTEN AND ANNE

AUTHOR'S PREFACE

THERE are two methods of teaching Zoology. One method is
to deal with a limited number of selected types one by one,
and the other is to compare corresponding parts of a number
of different animals. Each method has its advantages and
its drawbacks. The type method is essential for gaining
acquaintance with actual animals, and is of fundamental
importance from the fact that it permits of practical study of
the complete animals themselves. It cannot be too much
emphasised that Zoology is the study of animals, and not the
study of books written about them. That being so, it is
obviously more convenient to dissect and study one type
thoroughly before passing on to the next, than to have a
number of dissections of corresponding portions of several
animals all going on at the same time. The first two parts of
this book are devoted to a study of types carefully selected so
as to be of the greatest utility in the interpretation of other
forms. Part I deals with the adult structure, and Part II with
the modes of development.

While the type method is necessary for a start, it is attended
with certain dangers. Too much attention may be paid to the
types themselves and too little to the other animals of which they
are but only in a general way typical. There is also the danger
that " . . . a multitude of facts overcrowd the memory if they
do not lead us to establish principles. . . ." I have sought to
remedy this with the help of a comparative treatment of the
various organ-systems, which forms the subject of Part III.
In this part, the information obtained in Parts I and II is woven
into a framework, and other animals of interest are interpolated,
so as to present a general view of the organ-systems from the

evolutionary and functional points of view. By this means, it is possible to mention the significant points of certain animals which are unsuited to be taken as types in themselves. In many cases these interpolated animals are fossils, from the fragmentary knowledge of which it would be impossible to construct a sufficiently instructive type.

The use of this comparative treatment following upon the descriptions of types entails a certain amount of repetition, and this is intentional. Unfamiliar facts, which by themselves may be devoid of any particular interest, acquire an added attractiveness and significance when they are introduced under more than one setting.

Lastly, in Part IV the types and comparisons are woven together into a whole, and treated as a history of the chief groups of vertebrate animals. It is hoped that the general nature of the treatment of the characteristic features of vertebrates, and the inclusion of a section dealing with the affinities and evolution of the human race, may not be without interest for the human anatomist.

A few words may be added with regard to the types. They are selected and treated not only for their intrinsic importance, but also as introductions to the next types. The description of each type is therefore to some extent based on previous types. So the dogfish is not only an example of a primitive fish, but it also provides the material on which the disposition of the arterial arches and cranial nerves may be studied, and the knowledge so obtained is used in the interpretation of all higher types. Similarly, Gadus serves as an introduction to the bones of the skull, and Triton introduces the limb of the land-vertebrate. This must explain what may appear to be a lack of balance in the treatment of certain types.

Apart from the more ordinary dissections and observations which I have been able to make personally, I am indebted for sources of information chiefly to the teaching of the Oxford school of Zoology, and in particular to Professor E. S. Goodrich, F.R.S., whose principles I have largely attempted, however unsuccessfully, to follow. I wish to record my gratitude to him for his general guidance in many matters, and for the

facilities which I have enjoyed in the Department of Zoology and Comparative Anatomy of the Oxford University Museum.

On occasion, I have had the privilege of discussing certain matters with Professor G. Elliot Smith, F.R.S., Professor C. Judson Herrick, Professor J. P. Hill, F.R.S., Professor Sir Charles Sherrington, O.M., F.R.S., Professor W. J. Sollas, F.R.S., Professor A. Thomson, and Professor D. M. S. Watson, F.R.S. To all of them I wish to make due acknowledgment for the help which their information and advice have afforded me. To my friend and colleague Mr. B. W. Tucker I am especially indebted for reading the MS., and for making several valuable and helpful suggestions. I take great pleasure in recording my thanks to Professor Julian Huxley, without whose suggestion, interest, and persistent encouragement this book would have remained unwritten. It goes without saying that these gentlemen are not responsible for the errors which this book contains.

I have thought it inadvisable to burden the text with references. Instead, a short list of works is appended at the end of most of the chapters. I may mention here certain easily accessible works of great general utility in the study of vertebrates :

Abel, O. Die Stämme der Wirbeltiere. Berlin and Leipzig. 1919.

Brachet, A. Traité d'Embryologie des Vertébrés. Paris. 1921.

Graham Kerr, J. Text-Book of Embryology. Vol. II. London. 1919.

Hyman, L. H. A Laboratory Manual for Comparative Vertebrate Anatomy. Chicago. 1925.

Ihle, J. E. W., and others. Vergleichende Anatomie der Wirbeltiere. Berlin. 1927.

Jenkinson, J. W. Vertebrate Embryology. Oxford. 1913.

Kellicott, W. E. Chordate Development. New York. 1913.

Kingsley, J. S. Comparative Anatomy of Vertebrates. London. 1927.

Kingsley, J. S. The Vertebrate Skeleton. London. 1925.

Lull, R. S. Organic Evolution. New York. 1917.

von Zittel, K. A. Grundzüge der Paläontologie. Vol. II. Berlin. 1918.

With regard to the figures, I have preferred to illustrate a few points thoroughly, rather than attempt to provide a picture of all the structures that are worthy of attention. In any case, a picture is but a poor substitute for the structure itself. The majority of the figures were drawn specially for this book from dissections and laboratory preparations, and my intention has been to show that the student should have no difficulty in examining for himself the structures here figured (and many more besides which are not figured in this book), in any fairly-well equipped laboratory. I am indebted to my wife for preparing the figures for press, and to the following authors and publishers for permission to reproduce figures : to the Delegates of the Clarendon Press for figs. 73, 74, 75, 88, 89, 92, 94, 95, 96, 101, 102, 109, 110, 114, 115, 116, from J. W. Jenkinson's *Vertebrate Embryology*, and for permission to copy figs. 87, 90, 91, 93, 97, 98, 108, 113, from the same work ; to Professor G. Elliot Smith and Mr. Humphrey Milford for figs. 180, 181, 183, from *Essays on the Evolution of Man ;* to Professor Boule for fig. 182 ; to the Editor of the *Quarterly Journal of Microscopical Science* for permission to copy fig. 118 ; to Professor W. K. Gregory and the American Museum of Natural History for permission to copy part of fig. 158 ; to Professor L. Bolk for permission to copy fig. 123 ; to Professor W. J. Sollas for permission to copy fig. 182 ; and to Mr. B. W. Tucker and Mr. J. Z. Young for the loan of drawings of dissections.

In conclusion, I wish to express to Messrs. Sidgwick and Jackson my appreciation of the care and skill which they have so kindly shown in the preparation of this book.

G. R. DE B.

OXFORD,
February, 1928.

EDITOR'S INTRODUCTION

IT is the aim of this series to provide a number of text-books covering different fields of animal biology, in order to obviate as far as possible the pedagogically unfortunate habit of trying to introduce subjects of more recent development as appendages to a single morphological theme. We may deplore the way in which morphology arrogates to itself an unfair share of the time-table in many zoological laboratories in this country ; but the fact remains that morphology, well taught and well linked-up with other branches, is still educationally the best discipline in zoology, and, more surely than any other branch of the subject, throws open windows on to those long vistas that enlarge the mind and satisfy intellectual aspirations. But, even if its own fascination is brought out, it can be taught so as to leave it isolated among the later-developed branches of biology, like a foreign body encapsulated in living, growing tissues.

Mr. de Beer and I had many talks over this book. In the first place, we felt that the average zoology student to-day was being expected to absorb far too much detail in a given time, and that as a result, he was often overtaxed and prevented from seeing the wood for the trees. The teacher's aim should be to use no more fact-material than is needed to embody the architectural design which intellectual vision has planned ; but enough to build it firm, on lasting foundations.

Our second point was the need for linking up the various branches of biology. Morphology has such merits as a self-contained discipline that these efforts at liaison are not always made. I should like here to point out some of the ways in which an isolated morphology comes up against a blank wall, but through which she can advance to new view-points

once she has reached out her hand to sister branches of biology.

Morphology's central conception, Homology, is being modified by Genetics. Identical but independent mutation of genes, as is now recorded from several different species of Drosophila, shows that the conception of a common ancestor is no longer fundamental to the idea of homology.

Here we obviously approach orthogenesis. On the other hand, other orthogenetic ideas derived directly from morphological study melt away in the light of developmental physiology. Such phenomena as the progressive phylogenetic horn-development of various mammals, sometimes occurring independently in parallel stocks, need not after all imply orthogenesis in its strict sense of steady, determinate change of the germ-plasm. A study of the mechanism of the relative growth of parts shows, as Mr. de Beer points out (Chap. XLIII), that natural selection for increased size will automatically bring out the horn-growth, as what Darwin called a correlated variation.

Recapitulation too must be viewed differently as the result of studies on growth and on genetics. As D'Arcy Thompson pointed out in his *Growth and Form*, differences in proportion between related animals must be due primarily to differences in the growth-rates of the parts concerned. Later work has shown that the characteristic proportion of a part generally depends on the part continuing to grow at a different rate from the rest of the body for a long period. This being so, many cases of recapitulation are due solely to this differential growth. Schultz has shown that the fœtuses of primates still show the limb-proportions characteristic of their adults, but less strongly marked. This is recapitulation: but it is also a direct consequence of long-continued differential growth. The same principles can be applied to the recapitulation of shell-form shown in the ontogeny of many Nautiloids, Ammonites, etc., and to the fact that vestigial organs are often of greater relative size in young stages.

Such studies also bear on the systematic side of morphology ; for where the growth-rates of two parts are markedly

different, the animal has no fixed form. This is frequent in Crustacea and Insects, and may even occur in mammals, as Hinton has shown for voles. This obviously demands a revision of certain taxonomic ideas on the value of precise measurements of proportion.

The fact, first emphasised by Goldschmidt, that Mendelian factors frequently act by altering the rates at which developmental processes occur and the times at which they begin and end, rather than effecting qualitative changes *ab initio*, also bears on the problem. The eye of Gammarus is first scarlet, then darkens (at different rates according to the genes present) to or towards black. This is no proof that the ancestral eye was red, but depends on the physiology of melanin-deposition. Bolk, as a result of morphological study, has shown how frequently characters of early stages become prolonged into later life in the course of evolution ; his analysis enlarges the old concept of neoteny, and shows how much more common it is than usually supposed. This, however, is what the developmental physiologist would expect. If the time of appearance and relative importance of an organ depends upon the rate of some process, we are just as likely to have that rate altered in one direction as in the other, and therefore just as likely to have an embryonic character spread on to later stages as an adult character pushed back into earlier stages. The latter is recapitulation, the former the reverse ; and both depend, not upon some mysterious evolutionary urge, but upon simple developmental laws.

Other cases of recapitulation also become more intelligible in terms of other aspects of *Entwicklungsmechanik*. Why, for instance, are notochord, gill-slits, and arterial arches of amniote vertebrates recapitulated, while their limbs never recapitulate fins, and their gill-slits never recapitulate gills ? The answer seems simple. The recapitulated ancestral organs are necessities, as formative stimuli, for the production of adult structures ; the non-recapitulated ones are not.

" Racial senescence," so-called, is another morphological-evolutionary concept which looks very different when

morphology makes contact with physiology, but lack of space forbids a discussion of this point here.

Finally, there is the bearing on morphology of functional modification. Most biologists do not seem to realize the extent to which functional modification occurs in the normal vertebrate body. It appears to be true, not only that the size of every muscle in the body depends upon function, but the size, direction, and structure of every tendon and bone ; the detailed conformation of the blood-system depends largely, or perhaps wholly, on hydrodynamic considerations ; the size of every gland is regulated by its function ; and even the nervous system does not escape. It is only in earliest development that structure precedes function : later, structure is the resultant of function.

The recognition of these facts demands a new attitude towards the genetic and evolutionary bases of structural change. To take but one example, it is disturbing but true to find that the differences in form and minute architecture of the human heel-bone which distinguish it from that of apes are due to functional modification in each generation—to the fact that we put our weight on it in a different way owing to our walking upright. It is also disturbing to realize that in other groups, function does not play this important rôle in moulding structure. In all holometabolous insects, the size and form of all hard parts come into being once and for all, without previous function, since they have not existed in the larva, or been used in the pupa, and without the chance of being later modified by function, since there is no further moult. Thus definitive form—the morphologist's raw material—is arrived at by quite a different method in the two highest groups of animals.

I have, I hope, said enough to show that certain aspects of vertebrate morphology will bear restating ; and Mr. de Beer's pages are themselves the best evidence of his success in achieving that restatement without abandoning any of the essentials which give morphology such value as a discipline in its own right.

JULIAN S. HUXLEY.

CONTENTS

PART I

MORPHOLOGICAL TYPES ILLUSTRATING THE DIFFERENT STAGES OF ORGANISATION AND THE TREND OF VERTEBRATE EVOLUTION

xvi
CONTENTS

LIST OF ILLUSTRATIONS

VERTEBRATE ZOOLOGY

PART I

MORPHOLOGICAL TYPES

CHAPTER I

THE VERTEBRATE TYPE AS CONTRASTED WITH THE INVERTEBRATE

ALTHOUGH Vertebrate animals form the subject of this book, it must be said at once that, strictly, the term Chordate would be more correct as a title. The chorda dorsalis or notochord, from which the name is derived, made its appearance earlier in evolution than the vertebral column. There are therefore some animals which have a notochord but no vertebral column. On the other hand, all animals with a vertebral column also have a notochord at some time in their lives.

The term Vertebrate is used here partly because it is equivalent in importance to Invertebrate, and the most usual division of the animal kingdom lies between these two, and partly because attention is here paid particularly to the higher groups of " true " vertebrates. The lowly and peculiar Balanoglossids as well as the degenerate Ascidians will be left largely out of account, since they are not of much assistance in tracing the evolutionary history of the higher forms. Amphioxus as representative of the Cephalochordates, however, must be carefully considered on account of the help which it gives in interpreting and understanding various matters in higher forms.

B

The first necessity is to be clear as to what a chordate or vertebrate animal is, and how it differs in plan of structure from invertebrate animals (as typified, say, by Annelids or Arthropods).

A vertebrate is bilaterally symmetrical and moves typically in one direction with one side constantly presented upwards. A cœlom is present and the body, which is elongated from front to rear, is made up of a linear series of more or less similar blocks or segments. This repetition of parts or metameric segmentation affects tissues derived from all three of the primary layers from which the animal develops (see Chapter XI).

The gut on its way from mouth to anus is suspended in a fold of cœlomic epithelium forming a dorsal mesentery. The cœlomic cavity can be separated into the following regions. The dorsal parts of the cœlomic epithelium form the somites, which are segmentally arranged, and give rise to plates of muscle, or myotomes, one pair to each segment. The portion of cœlomic space associated with each myotome is a myocœl. The myocœl is bounded mesially by the myotome, and laterally by the cutis-layer of the cœlomic epithelium. Slightly ventral to each myotome is a region of cœlomic epithelium which gives rise to excretory tubes (cœlomoducts). This region is the nephrotome and its cavity the nephrocœl, also metamerically segmented. The ventral region of the cœlom is lined by epithelium (peritoneum) which forms the splanchnopleur where it is applied to the gut, and the somatopleur applied to the outer wall of the body. In this region the cavity is called the splanchnocœl.

The splanchnocœl is continuous from end to end of the animal, and uninterrupted by partitions or septa, except for that which separates an anterior pericardial from a posterior perivisceral space. This amounts to saying that the segmentation of the mesoderm does not persist in the ventral region. In higher forms much use is made of the free and uninterrupted space afforded by the splanchnocœl for the accommodation of longitudinal excretory and genital ducts, extensions of the liver and lungs, and coilings of the gut.
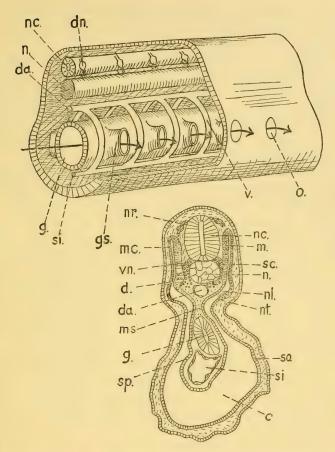
Fig. 1 (upper block).—Schematic view of a typical chordate animal in the region of the gill-slits.

Part of the wall of the body is represented as removed in order to reveal the interior.

Fig. 2 (lower block).—Transverse section through a typical chordate animal (an embryo dogfish).

c, splanchnocœl ; d, cutis-layer or dermatome ; da, dorsal aorta ; dn, dorsal nerve-root ; g, gut ; gs, gill-slit ; m, myotome ; mc, myocœl ; ms, mesentery ; n, notochord ; nc, nerve-cord ; nl, nephrocœl ; nr, neural crest ; nt, nephrotome ; o, opening of gill-slit ; sc, sclerotome ; si, sub-intestinal blood-vessel ; so, somatopleur or body-wall ; sp, splanchnopleur or gut-wall ; v, blood-vessel running in the gill-arch between the gill-slits ; vn, ventral nerve-root.

It is customary to refer to the dorsal segmented regions of the mesoderm as vertebral plate, and to the ventral unsegmented portions as lateral plate.

The gut is primitively straight, leading from a mouth at the anterior end to an anus ; the latter is not at the extreme posterior end of the animal but some distance in front of it. Behind the anus is a well developed tail containing tissue derived from all three germ-layers. The possession of such a structure is one of the characteristics of the type as opposed to most invertebrates.

The blood flows in well-marked channels, and the direction of flow is forwards ventrally and backwards dorsally, which is the reverse of the invertebrate condition. The heart is ventral. Blood is led from the intestine to the liver by a hepatic portal vessel. A " portal " vessel is a vein which differs from others in that it not only starts from capillaries, but breaks up into capillaries again at the other end. The hepatic portal vein therefore runs from the capillaries of the intestine to those of the liver, and " carries " digested food-products thither. Ordinary veins do not break up into capillaries again, but connect with other veins and lead to the heart.

The nervous system is in the form of a hollow tube which runs all the way down the dorsal side of the animal, and contrasts sharply with the chief invertebrate type of two solid ventral nerve-cords, swelling out into ganglia in each segment. In vertebrates, the nerves are of two kinds, issuing from the nerve-tube by dorsal or by ventral roots.

The primitive respiratory system of vertebrates is equally distinctive, and consists of a number (usually five or six) of pairs of openings which lead from the front part of the gut to the outside—the gill-slits with their contained gills. These structures are among the most important, not only on account of their distinctiveness, but also because of the modifications which they undergo and the consequences which follow from their possession in evolution. The higher vertebrates breathe by means of lungs, which are sacs pushed out from the gut.

Running down the back of the animal, above the gut and

beneath the nerve-tube, is a slender elastic rod which acts as a primitive skeleton. This is the notochord, which in higher forms is more or less obliterated and replaced by the backbone or vertebral column. The main skeleton of vertebrates is internal and not outside the body as in many invertebrates.

The higher forms have appendages, either fins or limbs, four in number arranged in two pairs. They are composed of tissue derived from several segments, not from one only as in invertebrates.

The differences and similarities between this fundamental plan and that of invertebrates may conveniently be set out in tabular form.

Vertebrates and most higher Invertebrates agree in being :
    bilaterally symmetrical ;
    cœlomate ;
    metamerically segmented.

Vertebrates differ from Invertebrates in having :
    a notochord ;
    a dorsal and tubular nerve-cord ;
    gill-slits ;
    a postanal tail ;
    a ventral heart through which blood flows forwards ;
    main skeleton internal ;
    appendages formed from several segments ;
    a hepatic portal system ;
    dorsal and ventral nerve-roots.

CHAPTER II

AMPHIOXUS, A PRIMITIVE CHORDATE

A THOROUGH knowledge of the type which forms the subject of this chapter is fundamental for the study of vertebrates.

Externals.—Amphioxus lanceolatus is a small animal (about 2 inches long) found in shallow seas with a sandy bottom in which it burrows. It is elongated and pointed at each end, from which fact it derives its name. The body is compressed from side to side and is capable of rapid movement by swimming, though it usually stays embedded in sand, feeding with only the mouth protruding. Both ends of
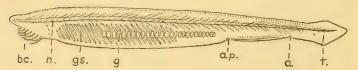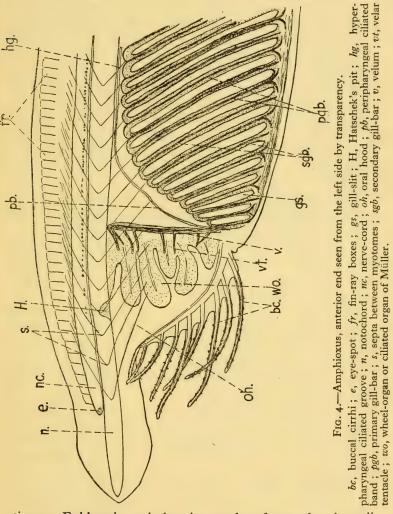
FIG. 3.—Amphioxus seen from the left side.

a, anus ; *ap*, atriopore ; *bc*, buccal cirrhi ; *g*, gonad ; *gs*, gill-slits ; *n*, notochord ; *t*, tail.

the animal are expanded into thin vertical fins, which are joined by a shallow fin running all along the middle line of the back. The fin also extends a short distance forwards from the hind end on the ventral side. This median fin is of simple structure ; it is supported by a row of stiffeners known as " fin-ray boxes." These are made of connective tissue, and they are more numerous than the segments of the body. Along the dorsal fin the fin-ray boxes are arranged in a single row, but along the short ventral fin there is a double row of fin-ray boxes.

6

The epidermis is only one-cell thick, as in many invertebrates. Underlying the epidermis is the mesodermal dermis, which, in Amphioxus, takes the form of gelatinous connective

FIG. 4.—Amphioxus, anterior end seen from the left side by transparency.

bc, buccal cirrhi; *e,* eye-spot; *fr,* fin-ray boxes; *gs,* gill-slit; H, Hatschek's pit; *hg,* hyperpharyngeal ciliated groove; *n,* notochord; *nc,* nerve-cord; *oh,* oral hood; *pb,* peripharyngeal ciliated band; *pgb,* primary gill-bar; *s,* septa between myotomes; *sgb,* secondary gill-bar; *v,* velum; *vt,* velar tentacle; *wo,* wheel-organ or ciliated organ of Müller.

tissue. Epidermis and dermis together form what is ordinarily known as the skin. Beneath the skin the myotomes of the body are arranged in a continuous row from front to rear.

Seen from the side and visible through the skin they are markedly V-shaped, with the apex pointing forwards. Those of one side alternate with those of the other.

The ventral side of the front end of the animal is expanded to form the oral hood. The sides of the oral hood (which are not quite symmetrical) bear a fringe of buccal cirrhi, each one supported by a small jointed skeleton. The cirrhi bear sense-organs. On the under surface of the oral hood the epithelium is modified in places into a ciliated organ (the organ of Müller, or wheel-organ) whose function it is to create a current of water flowing towards the mouth. Slightly to the right of the middle line, a small depression opens into the cavity of the oral hood, known as Hatschek's pit. (The development of this interesting structure is described on p. 167.)

The mouth is situated at the hind end of the oral hood, and is a circular aperture pierced through a vertical transverse plate, the velum. The size of the opening is regulated by a circular sphincter muscle. In addition, there are twelve velar tentacles arising from the rim of the mouth, provided with sense-organs. Their function is to act as a strainer across the mouth-opening.

The anus opens not at but near the hind end of the body on the ventral surface, slightly to the left of the middle line owing to median position of the ventral fin. Just in front of the ventral fin is another aperture, the atriopore, the significance of which will be understood with a knowledge of the structure of the atrium.

Other external features to be noticed are the olfactory (or Kölliker's) pit on the left side of the body very near the front end, and the metapleural folds of the atrium. The gonads can also be seen from the outside, as a row of sacs between the mouth and the atriopore.

Alimentary System.—The gut leads straight from the mouth to the anus without any loops or kinks. The anterior half of it is the pharynx, the posterior is the intestine. A blind outpushing is given off on the right side from the front of the intestine, forming the so-called liver-diverticulum.
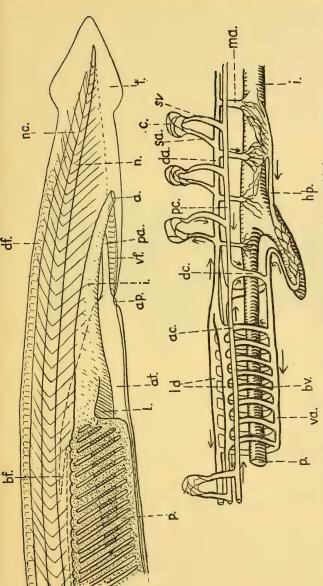
FIG. 5 (upper block).—Amphioxus : hinder end seen from the left side by transparency.

a, anus ; *ap*, atriopore ; *at*, atrial cavity ; *bf*, brown funnel ; *df*, dorsal fin-ray boxes ; *i*, intestine ; *l*, liver ; *n*, notochord ; *nc*, nerve-cord ; *p*, pharynx ; *pa*, posterior extension of the atrium ; *t*, tail-fin ; *vf*, ventral fin-ray boxes.

FIG. 6 (lower block).—Amphioxus ; diagram illustrating the vascular system.

ac, anterior cardinal vein ; *bv*, branchial vessel running in gill-bar ; *c*, capillaries ; *da*, dorsal aorta ; *dc*, ductus Cuvieri ; *hp*, hepatic portal vein ; *i*, intestine ; *ld*, lateral dorsal aorta ; *ma*, artery running in the mesentery and supplying the gut ; *p*, pharynx ; *pc*, posterior cardinal vein ; *sa*, segmental artery ; *sv*, segmental vein ; *va*, ventral aorta.

The gut is suspended by a dorsal mesentery, and its lining is ciliated. It is surrounded by a thin coat of smooth muscle.

The side walls of the pharynx are perforated by a large number of gill-slits, openings which slant forwards from below up. For this reason several gill-slits will be cut in a single transverse section.

Ciliary Mode of Feeding.—Along the whole length of the dorsal wall of the pharynx runs a ciliated groove known as the
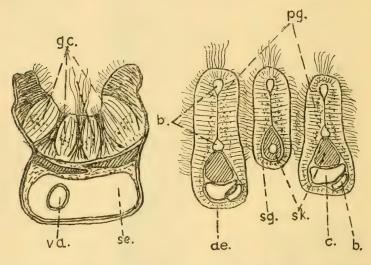
FIG. 7.—Amphioxus : transverse section through the endostyle showing the cilia, the four tracts of glandular cells (*gc*), the subendostylar cœlom (*se*), and the ventral aorta (*va*).

FIG. 8.—Amphioxus : transverse section through two primary (*pg*) and one secondary (*sg*) gill-bars.
ae, atrial epithelium ; *b*, blood-vessel ; *c*, cœlomic cavity in the primary gill-bars ; *sk*, skeletal rods of the gill-bars.

hyperpharyngeal groove. Anteriorly this groove connects with two tracts of ciliated cells, the peripharyngeal bands which pass round one on each side behind the mouth and down to the floor of the pharynx. There they join the endostyle, which extends all the way back through the pharyngeal region. The endostyle consists of four tracts of glandular cells, separated by tracts of ciliated cells. The glandular cells secrete a sticky mucus which, by the action of the cilia, is

driven forwards and sideways up the gill-bars, and round the peripharyngeal bands, where food particles become entangled in it. The food particles have been swept into the mouth with the current of water made by the cilia of the wheel-organ and gill-bars. Mucus and food then get carried into the hyperpharyngeal groove and back to the intestine. By this means the food is carried safely back through the pharynx as by a moving stairway, and is not lost with the water which streams out through the gill-slits.

The ciliary method of feeding is primitive. From the nature of its mechanism it can only supply particles of food
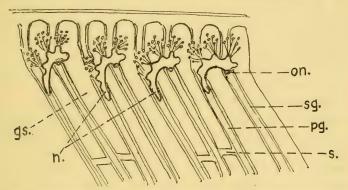
FIG. 9.—Amphioxus : view of the dorsal portion of the pharynx and gill-slits (*gs*), showing the nephridia (*n*).

on, opening of the nephridium into the atrium ; *pg*, primary gill-bar ; *s*, synapticulum ; *sg*, secondary gill-bar.

of small size, and therefore it can only occur in smallish animals. In higher forms in which other methods such as biting or sucking have been adopted for procuring food, the endostyle is no longer required to secrete a mucus "fly-paper"; it becomes modified in a most striking way and gives rise to the thyroid gland (see p. 399).

Atrium.—The gill-slits do not open directly to the outside world but into a cavity known as the atrium, which in its turn opens to the exterior near its posterior extremity by the atriopore. On the right side of the body (but not on the left) the atrium extends back behind the atriopore as a blind sac

nearly as far as the anus. The atrium has been formed by folds of the body-wall above the gill-slits growing down on each side (the metapleural folds) and meeting underneath what is the true ventral surface of the animal. The space of the atrium therefore represents a portion of the outside world, and is lined entirely by ectoderm. The low ridges running along the ventro-lateral edge of each of the atrial folds are the metapleural folds, and between them, meeting in the middle line, are the epipleurs, in the form of horizontal shelves. These close off the atrial cavity (see p. 170). The atrium is closed in front so that all the water which enters it does so through the gill-slits and passes out of the atriopore. Where the pharynx passes into the intestine, a pair of conical outpushings of the atrium project into the dorsal cœlomic cavities, one on each side, forming the so-called " brown funnels " (see p. 15). The function of the atrium is to protect the pharyngeal region, which is very vulnerable owing to the gill-slits.
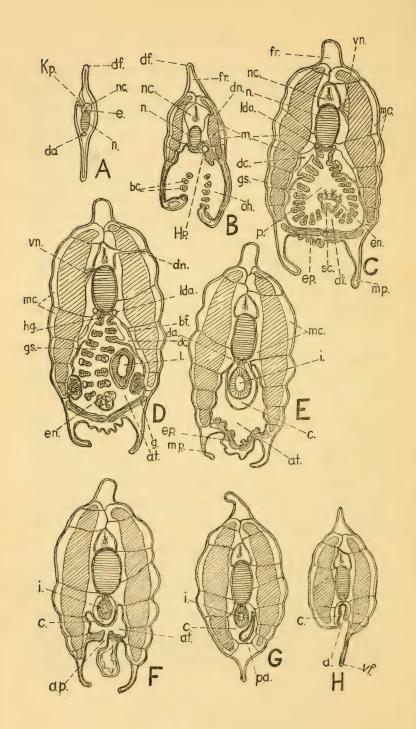
Respiratory System.—At early stages the gill-slits corresponded to the segmentation of the body, but more and more of them are formed (up to 180) and the correspondence is lost. The gill-slits are separated from each other by gill-bars, the inner surface of which is covered by endodermal, the outer by ectodermal tissue (forming the inner wall of the atrium). There are two kinds of gill-bars: primary, and secondary or tongue-bars. All the bars have a skeletal rod (composed of a chitin-like substance) passing down them and stiffening them. The rods of the secondary bars end simply at their ventral ends, while those of the primary bars bifurcate. Another difference is that the primary bars contain a portion of cœlomic cavity while the secondary bars do not. The bars are strongly ciliated, and by the activity of these cilia water is forced through the slits into the atrium. As the water passes between the gill-bars, the blood circulating in the blood-vessels of the latter becomes oxygenated. There are three vessels in each primary bar and two in each secondary bar ; the vessels in the secondary bars are connected with those in the primary bars by vessels running in the synapticula, or connecting struts.

Vascular System.—Running forward under the floor of the pharynx beneath the endostyle is the ventral aorta. There is no specialised heart, but this aorta is contractile, and propels the blood into the afferent branchial arteries which run to the primary gill-bars. At the base of the bars these arteries swell into little contractile bulbils and divide into the three vessels which run up the bars. The secondary bars obtain blood in their two vessels indirectly from the primary bars through the vessels in the synapticula. Branches are sent to the excretory organs (nephridia, see p. 15) which are thereby enabled to extract the excretory products from the blood.

From the gill-bars the blood is collected into the efferent branchial vessels which run to the lateral dorsal aortæ, one on each side of the mesentery, just above the hyperpharyngeal groove. Behind the pharynx they join to form the single dorsal aorta, which carries blood back to the posterior regions of the body. In the septa separating each pair of adjacent myotomes, segmental vessels leave the aorta and distribute blood locally. The blood is collected up again into the sub-intestinal vessel which runs forwards beneath the intestine from the hind end of the body. It breaks up into capillaries in the region of the liver-diverticulum, and so forms a hepatic portal system. From the liver the vessel runs forwards beneath the endostyle of the pharynx as the ventral aorta. There are also paired cardinal veins running in the body-wall at the level of the gonads, and extending forwards in the region of the pharynx and backwards to the tail. These veins connect with the subintestinal vessel by transverse veins, the ductus Cuvieri, on each side, which bridge across the cœlom. The blood is colourless.

Cœlom.—The relations of the cœlom are of great importance. The myotomes of the body are separated by septa (between the segments), but they do not fit the septa closely. Small spaces are left which are remnants of the myocœls.

Behind the pharynx the relations of the cœlom are quite simple and typical. The gut is suspended by a dorsal mesentery in a spacious splanchnocœl. In the pharyngeal region, however, the relations are slightly complicated by the

presence of the gill-slits. Since these slits are openings from the gut to the outside (morphologically, ignoring the atrium) they form connexions between the gut-wall and the body-wall, and thereby necessarily obliterate the cœlom in places. The cœlom, therefore, is restricted to the regions between the slits, *i.e.* to the gill-bars. The cœlom is perfectly normal above and below the level of the gill-slits. Accordingly, there are a pair of dorsal cœlomic cavities, separated from one another in the middle line by the dorsal mesentery; and a ventral cœlomic cavity known from its position as the sub-endostylar cœlom. The latter is in open communication with the dorsal cœloms on each side by means of the cœlomic canals in the primary gill-bars. There are no cœlomic canals in the secondary or tongue bars, for they are later developments which divide the original gill-slits into two. The relations of the cœlom are not difficult to understand when it is remembered that relicts are left between the slits in the primary gill-bars.

Into each dorsal cœlomic cavity a conical outpushing of the atrium projects, from the region just behind the gill-slits. The apex of the cone points forwards, and so lies dorsal to the hindmost gill-slits. These structures are the so-called " brown funnels," of doubtful significance (see p. 12).

Excretory System.—The excretory organs of Amphioxus are remarkable in that they are nephridia. In all other chordates the excretory organs are cœlomoducts or meso-dermal kidneys (see p. 31). The nephridia lie over the gill-slits, project into the dorsal cœlomic cavities and extend a short way down the cœlomic canals in the primary bars in the

---

Fig. 10.—Amphioxus : transverse sections through the body in the regions of A, Kölliker's pit ; B, Hatschek's pit ; C, the anterior region of the pharynx ; D, the posterior region of the pharynx ; E, between pharynx and atriopore ; F, the atriopore ; G, between atriopore and anus ; H, the anus.

a, anus ; *ap*, atriopore ; *at*, atrium ; *bc*, buccal cirrhi ; *bf*, brown funnel ; *c*, cœlom ; *da*, dorsal aorta ; *dc*, dorsal cœlomic canal (in the region of the pharynx) ; *df*, dorsal fin ; *dn*, dorsal nerve-root ; *e*, eye-spot ; *en*, endostyle ; *ep*, epipleur ; *fr*, fin-ray box ; *g*, gonad ; *gs*, gill-slit ; *hg*, hyperpharyngeal ciliated groove ; *Hp*, Hatschek's pit ; *i*, intestine ; *Kp*, Kölliker's pit ; *l*, liver ; *lda*, lateral dorsal aorta ; *m*, myotome ; *mc*, myocœl ; *mp*, meta-pleural fold ; *n*, notochord ; *nc*, nerve-cord ; *oh*, oral hood ; *p*, pharynx ; *pa*, extension of the atrium behind the atriopore ; *sc*, subendostylar cœlomic canal ; *vf*, ventral fin ; *vn*, ventral nerve-root.

form of small bent tubes. Each nephridium bears bunches of flame-cells or solenocytes, like hollow pins with a whip or flagellum hanging down inside from the head, and serving to flush out the contents. There is no internal opening to the nephridia, which derive the products which they excrete from the blood-vessels and cœlomic fluid by diffusion. The nephridia open into the atrium (that is, morphologically to the outside) by small pores situated near the top of the secondary gill-bars. They are segmental in origin.

There is another nephridium at the front of the animal, lying dorsal to the oral hood near the middle line. It opens into the pharynx just behind the mouth, and is known as Hatschek's nephridium. No chordates other than Amphioxus are known to possess nephridia.

Genital System.—The sexes are separate, but very similar in appearance. The gonads are pouches of germ-cells arranged in a row on each side of the body from about the 10th to the 36th segments, in the region of the gill-slits. When these pouches are full they bulge into the atrium ; but they must not be considered as lying in the atrium, for they are separated from it by the whole thickness of the body-wall. The segmental arrangement of the pouches is more or less preserved. When ripe, the germ-cells burst out of the pouches and pierce the body-wall, thus finding themselves in the atrium. From here they make their way to the outside through the atriopore. The cavity of the pouches is, of course, cœlomic.

Skeleton.—Reference has already been made to the skeletal supports of the buccal cirrhi and to those of the gill-bars. The most important skeletal structure of Amphioxus is, of course, the notochord. This elastic rod extends from end to end of the animal, dorsal to the gut and ventral to the nerve-cord. Its extreme extension, almost to the tips of the anterior and posterior fins, is noteworthy.

Nervous System.—The central nervous system consists of a straight tube running all the way down the back of the animal, dorsal to the notochord and ventral to the fin-ray boxes. Kölliker's pit on the left side of the snout represents

the spot where the cavity of the tube opened to the exterior at earlier stages (the neuropore).

The cavity of the nerve-tube is enlarged at its front end forming the cerebral vesicle. At the same time the external diameter of the tube remains the same; its walls are here therefore thinner. This specialisation is in Amphioxus the only indication of a brain. At the front end of the nerve-tube is a pigment-spot, to be regarded as a visual organ. Other such pigment-spots, or primitive " eyes," are to be found further back near the central canal.

On each side of the body the nerve-cord gives off nerves, which are of two kinds, dorsal and ventral. In each segment on each side of the body there is one dorsal nerve-root and one bunch of ventral nerve-roots. The ventral roots are distributed solely to the muscle-fibres in the myotome of that segment, and are " motor " nerves. The dorsal roots are concerned with transmitting impulses received from the sense-organs all over the skin (especially numerous on the buccal cirrhi), and with innervating the smooth musculature of the gut and atrium. The axons which go to make up the sensory or afferent fibres of the dorsal nerve-roots are derived directly from the sensory cells in the skin. The sensory cells therefore convey their impulses direct to the central nervous system on the plan characteristic of many invertebrates. In all forms above Amphioxus, the impulses are collected from the sensory cells by axons derived from other nerve-cells, whose nuclei lie in swellings or ganglia on the dorsal nerve-roots. Amphioxus is therefore primitive in not possessing these ganglia or nerve-cells.

The most anterior two pairs of roots are dorsal, and have no ventral roots corresponding to them. They innervate the sense-organs of the snout, oral hood, and buccal cirrhi.

While reviewing the foregoing description of Amphioxus an important analysis can be made. In the light of knowledge of other forms, the characteristics of an animal can be divided into two classes : primitive and specialised. There are those characters which are developed and perfected in the process of evolution to the next stage, and which are therefore simpler

C

at the stage in question (in this case Amphioxus).   A primitive character of this kind is shown by the vascular system of Amphioxus.   There are also negative characters, for the later evolutionary stage may possess structures which the present stage lacks.   The absence of a specialised head in Amphioxus is an example of a primitive negative character of this kind. Then there are characters of which it cannot be said that they are simpler than those of the next evolutionary stage, nor that they lead on to them, but which can be considered as historically primitive in the sense that they occur at early stages but not at later ones.   The ciliary method of feeding is an historically primitive character of this kind : it preceded the jaw-method of feeding in time, but was not simpler than the latter method, nor did it lead up to it.

All primitive characters imply the possibility of progress in evolution.   On the other hand, there are certain characters which have not only not contributed to the progress in evolution to the next stage, but have debarred their possessors from ever evolving to that stage.   Such specialised or secondary characters are typified by the atrium of Amphioxus.

The analysis may conveniently be set out in tabular form :

Amphioxus

Primitive Characters.

> Ciliary mode of feeding, with endostyle ;
> Epidermis one-cell thick ;
> Afferent nerve-fibres derived from sensory cells ;
> Complete row of segmented myotomes from front to rear ;
> Very slight specialisation of brain ;
> No specialised head ;
> No paired limbs or paired sense-organs ;
> No specialised heart ;
> Gonads segmental, without special ducts ;
> Nephridia ; segmentally arranged ;
> Simple and unbranched liver diverticulum.

Specialised Characters.

> Atrium ;
>
> Extra large number of gill-slits, having lost corre-
> spondence with the segmentation of the body ;
>
> Tongue-bars ;
>
> Asymmetry of oral hood and early development ;
>
> Extreme anterior extension of the notochord.

The large number of its primitive characters show that
Amphioxus is a primitive animal, *i.e.* related to the original
ancestors from which all chordates evolved. The secondary
characters which Amphioxus possesses, however, show that
it is not on the direct line of chordate descent.

LITERATURE

BOURNE, G. C.   An Introduction to the Study of the Comparative Anatomy
of Animals.   Vol. 2.   Bell, London, 1915.

DELAGE, Y., ET HEROUARD, E.   Zoologie Concrète.   Vol. 7.   Les
Procordés.   Schleicher Frères, Paris, 1898.

GOODRICH, E. S.   On the Structure of the Excretory Organs of Amphioxus.
Quarterly Journal of Microscopical Science.   Vol. 45, 1902 ;   and
Vol. 54, 1910.

ORTON, J. H.   The Ciliary Mechanisms on the Gill and the Mode of
Feeding in Amphioxus.   Journal of the Marine Biological Association.
Vol. 10, 1913.

WILLEY, A.   Amphioxus and the Ancestry of the Vertebrates.   Columbia
University Press, 1894.

CHAPTER III

Externals.—Petromyzon, commonly known as the lamprey, is an elongated animal not unlike a fish, but without paired fins or jaws. Some species live in fresh water, and others in the sea. Their length varies from a few inches to about four feet.

The slimy epidermis is about a dozen cells in thickness and contains glands. In the middle line the skin is produced into median fins, two on the back and one round the tail. These fins are stiffened only by rays of cartilage.
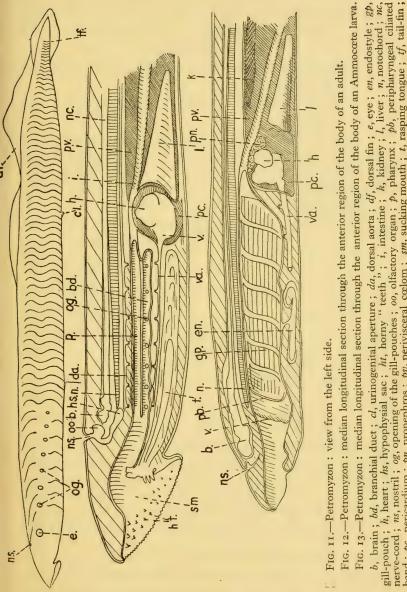
At the front there is a circular mouth surrounded by horny teeth. Behind the mouth on each side is a small deep-set eye, and then seven apertures in a row. These are the external openings of the gill-pouches. Dorsally, in the middle line near the front, there is a small hole which is the single median opening of the nasal sacs and the hypophysial cavity (see p. 401). The anus is in the mid-ventral line, not far in front of the ventral portion of the tail-fin.

Through the mouth there protrudes a rasping organ called the tongue, which like the sides of the mouth is covered with horny teeth. These teeth are little cones, formed from the ectoderm, and replaced from underneath when worn away. They must be carefully distinguished from the teeth of all higher forms, which are of a different nature.

The lamprey fastens itself by means of its circular and sucker-like mouth on to its food (mostly fish), and rasps at it with its tongue. This method of feeding is very specialised and almost degenerate ; and it has brought about several specialisations in the structure of the animal. The horny teeth are one of these.

Fig. 11.—Petromyzon : view from the left side.

Fig. 12.—Petromyzon : median longitudinal section through the anterior region of the body of an adult.

Fig. 13.—Petromyzon : median longitudinal section through the anterior region of the body of an Ammocoete larva.

b, brain ; bd, branchial duct ; cl, urinogenital aperture ; da, dorsal aorta ; df, dorsal fin ; e, eye ; en, endostyle ; gp, gill-pouch ; h, heart ; hs, hypophysial sac ; ht, horny "teeth" ; i, intestine ; k, kidney ; l, liver ; n, notochord ; nc, nerve-cord ; ns, nostril ; og, opening of the gill-pouches ; oo, olfactory organ ; p, pharynx ; pb, peripharyngeal ciliated band ; pc, pericardium ; pn, pronephros ; pv, perivisceral cœlom ; sm, sucking mouth ; t, rasping tongue ; tf, tail-fin ; v (in Fig. 12), ventricle ; v (in Fig. 13), velum ; va, ventral aorta.

Head.—The outstanding advance which the lamprey shows over the condition of Amphioxus is the possession of a definite head. A head is a specialisation of the anterior region of the body brought about in connexion with :

> the development of paired sense-organs for perception at a distance ;
>
> the correlated specialisation of the nerve-tube into a brain.

To these is added in higher forms the specialisation of the most anterior gill-bars into jaws for the capture of food ; but this need not be considered here as the lamprey has no jaws. The organs of the head are protected by a special skeletal structure called the skull.

Sense-Organs.—The nose consists of two sacs invaginated from the skin, and whose epithelium is specialised for the perception and detection of chemical substances. This epithelium sends nerve-fibres to the brain, forming the olfactory nerves. While the paired nature of the olfactory organ is easily seen on dissection, it is outwardly obscured by the great expansion and upgrowth on each side of the region corresponding to the upper lip. This modification causes both the nasal pits and the hypophysial sac to open to the outside by a single common median dorsal pore.

The main rudiments of the paired eyes in development grow out from the brain on each side, giving rise to the optic vesicles. The outer side of each vesicle is pushed in so as to convert it into a cup, and the lens (developed from the superficial skin) fits into the mouth of the cup, just beneath its rim. The inner layer of the cup contains the cells which are sensitive to light, and form the retina ; the outer layer forms a backing of pigment. Outside this again, two mesodermal layers are laid on. The innermost of these is the choroid which contains blood-vessels, the outer, which is also the outermost of the whole eyeball, is the hard and protective sclerotic. The sclerotic encloses the whole eyeball, but in front of the lens it is transparent, forming the cornea. The cornea is in contact with the epidermis, which is here also transparent, forming the

conjunctiva. The eye may then be regarded as a closed hollow ball, with the enclosed chamber divided into two by the lens :
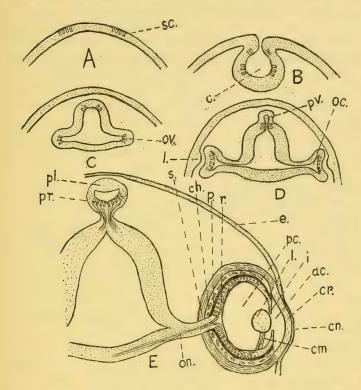
FIG. 14.—Diagram showing the method of origin of the eyes in chordate animals and the relations of the sensory cells.

A, before the formation of the nerve-cord the sensory cells (*sc*) are on the outer surface ; B, when the nerve-cord has been formed the sensory cells line its cavity (*c*) ; C, formation of the optic vesicles (*ov*) ; D, origin of the lens (*l*) from the epidermis, conversion of the optic vesicles into optic cups (*oc*) and formation of the pineal vesicle (*pv*) ; E, condition with completely formed eyes. *ac*, anterior chamber ; *ch*, choroid ; *cm*, ciliary muscle ; *cn*, conjunctiva ; *cr*, cornea ; *e*, epidermis ; *i*, iris ; *l*, lens ; *on*, optic nerve ; *p*, pigment layer ; *pc*, posterior chamber ; *pl*, pineal lens ; *pr*, pineal retina (erect) ; *r*, retina (inverted) ; *s*, sclerotic.

viz., a posterior chamber between the retina and the lens, and an anterior chamber between the lens and the cornea. The posterior chamber contains a jelly-like substance called the

vitreous humour, the anterior chamber contains the aqueous humour.

There is an important point to notice in connexion with the retina. In Amphioxus the cells which are sensitive to light line the central canal of the nerve-tube ; in all higher forms, that portion of the wall of the nerve-tube in which these cells lie is bulged out sideways to form the eye. The sensitive cells are, however, still morphologically on the inner side of the wall of the brain (*i.e.* adjacent to the central cavity or the cavity of the optic vesicle). The nerve-fibres which convey the impulses away from the retina cannot go through this cavity, they must run in the wall of the optic vesicle and of the brain. In so doing the nerve-fibres must therefore pass between the sensitive cells and the lens. This means that the image of the seen object reaches these sensitive cells after passing through the nerve-fibres. A retina of this kind is called inverted, and is characteristic of the paired eyes of all chordates. The pineal eyes (described below in connexion with the brain) have an erect retina, for here the nerve-fibres leave the retina on the side away from the lens. With regard to the paired eyes, it is essential to realise that the cavity of the primitive optic vesicle is not the same as that of the definitive eyeball (or posterior chamber). In the process of conversion of the optic vesicle into the optic cup, the cavity of the vesicle has been obliterated. The eyes are not immovable, but can be turned in various directions. This is effected by the myotomes of the first three segments, which are modified into so-called eye-muscles. The description given above applies to the paired eyes of all chordates ; the eyes of the lamprey are, however, somewhat degenerate.

Petromyzon has so-called auditory organs or ears, but it must be remembered that these organs primitively do not serve for the purpose of hearing, but are organs of balance. They take the form of sacs on each side of the brain behind the eyes, giving off canals in the form of half-hoops, each end of which opens into the sac. These are the semicircular canals ; each one bears a swelling or ampulla containing a statolith or organ of balance (see p. 395). In all vertebrates above Petromyzon

there are three such canals, in planes at right angles to one another, but Petromyzon has only two.

Brain.—The anterior end of the nerve-tube is modified and enlarged in connexion with the paired sense-organs to form the brain. The brain can be divided into three main regions : fore-, mid-, and hindbrain. The forebrain bears the olfactory lobes in front, and on each side it connects with the eyes (which are really part of it) by the optic nerves. The roof bears the pineal and parapineal eyes. These lie in the middle line, the pineal above the parapineal which is degenerate. The pineal eye is a vesicle of which the dorsal wall forms a lens, and the ventral wall a retina backed with pigment. The nerve-fibres
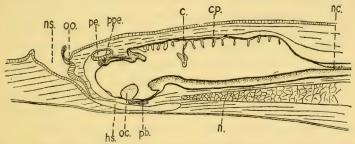
Fig. 15.—Petromyzon : view of median longitudinal section through the brain.

c, cerebellum ; *cp*, choroid plexus ; *hs*, hypophysial sac ; *n*, notochord ; *nc*, nerve-cord ; *ns*, nostril ; *oc*, optic chiasma ; *oo*, olfactory organ ; *pb*, pituitary body ; *pe*, pineal eye ; *ppe*, parapineal eye.

lead away from the underside of this retina, which is therefore not inverted but erect. Above the pineal eye, the skull is thin and the tissues are more or less transparent. Beneath the forebrain is a simple pituitary body (see p. 399), the pars intermedia of which is apposed to the feebly developed infundibulum of the brain. The pituitary body in Petromyzon has lost connexion with the hypophysial cavity ; the latter extends backwards beneath the brain forming the hypophysial sac, and connects with the exterior through the median dorsal pore.

The midbrain bears the optic lobes, and the roof of the hindbrain is modified into a rudimentary cerebellum. It is

important to notice that the roof of the brain in Petromyzon is very thin and membranous ; with the exception of the transverse commissures in the forebrain, the optic lobes, and the cerebellum, it contains scarcely any nerve-cells at all.

Although at first sight the brain differs considerably from the more posterior part of the nerve-tube or spinal cord, it is easy to see how it was derived from the latter.

In each segment on each side there is a ventral nerve supplying the segmented muscles formed from the myotomes of the vertebral plate (somatic muscles), and a dorsal nerve supplying the sense-organs. In the gill-region, the dorsal nerves also supply the muscles formed from the unsegmented lateral plate (visceral or splanchnic muscles). In the region of the trunk these segmental nerves are called spinal nerves, those which emerge from the brain are called cranial nerves.

Nerves.—The ventral nerves of the first three segments innervate the muscles which actuate the eyeball. They are respectively the oculomotor, trochlear, and abducens. The dorsal nerves corresponding to them are the profundus, trigeminal, and facial ; the auditory nerve is a branch of the facial. The ventral root of the 4th segment supplies the most anterior complete myotome, and its corresponding dorsal nerve, the glossopharyngeal, passes down in the arch behind the first gill-slit (and in front of the second). The next dorsal nerve, the vagus, is a composite one, formed by the aggregation of portions of several other posterior dorsal nerves. It sends a branch down behind each of the remaining gill-slits, as well as to the " lateral-line " organs (see p. 38), and to the heart and gut. The ventral roots corresponding to the vagus supply the 5th and following myotomes, and the muscles beneath the gills. The muscles of the tongue are supplied by the trigeminal nerve.

In Amphioxus, the dorsal or sensory nerves are formed of fibres produced inwards from the sensory cells themselves. In Petromyzon and all higher forms this method of formation applies only to the olfactory nerves. All the other sensory nerves are formed in a different way. There are special nerve-cells which send one fibre to the sensory cell and another

into the central nervous system. These nerve-cells are not in the nerve-tube but just outside it. They lie on the track of the sensory dorsal nerves and form swellings or ganglia. In Petromyzon and all higher forms, on every dorsal nerve-root, whether cranial or spinal, there is a ganglion. The ventral nerves consist of nerve-fibres which are formed from nerve-cells which lie inside the nerve-tube ; they therefore do not have ganglia.

In Petromyzon there are two important primitive features to note in connexion with the nerves. One is that the dorsal and ventral roots of each segment do not join together, but remain separate. The other is that the nerves are simple and uncovered by insulating material, *i.e.* they are non-medullated.

The nerves which innervate striated muscles go straight from the central nervous system to the muscle. On the other hand, those nerves which supply the smooth muscle-fibres of the gut and of the arteries (and in higher forms certain other structures also) do not run direct from the central nervous system to the muscle. Instead, they run to other nerve-cells, and these run to the muscle. These latter nerve-cells form part of the autonomic nervous system (see Chapter XXXI). In Petromyzon this system is only feebly developed. It is represented by some groups of nerve-cells along the gut, supplied by the intestinal branch of the vagus (see p. 47), and also by some cells close to blood-vessels near the spinal cord.

Skull and Skeleton.—The brain, paired sense-organs, and roots of the cranial nerves are protected by a case of cartilage forming the skull. This is characteristic of all forms above Amphioxus which are therefore referred to as Craniata. The brain is surrounded by the cranium proper ; the sense-organs are protected by capsules. The nasal capsules are fixed on to the front of the cranium by connective tissue ; the auditory capsules are firmly fused on to the sides of the cranium by cartilage. The spinal cord enters the skull at the hind end through the foramen magnum, but in Petromyzon the nerves of the fourth and following segments (glossopharyngeal and vagus) come out from the brain behind the hindmost limit of the skull. This shows that the process of cephalisation or

specialisation of the skull has not extended very far. The walls of the skull are very incomplete, as is the roof. The notochord extends forwards as far as the forebrain. In the trunk-region, in each segment on each side of the notochord, is a pair of cartilaginous pegs, one behind the other. The anterior peg in each segment (interdorsal) is in front of the ventral nerve-root ; the hinder peg (basidorsal) is in front of the dorsal root. These pegs are the rudiments of the vertebral column, as yet very incomplete and not in any way constricting or interrupting the notochord.

Between every two gill-slits, behind the last and in front of the first, are cartilaginous rods, the branchial arches or gill-arches. Together they constitute the branchial basket. The most anterior branchial arches, together with cartilages belonging perhaps to vanished gill-clefts and others in connexion with the rasping tongue, form a skeletal framework attached to the skull and termed the splanchnocranium. The brain-case and sense-capsules are called the neurocranium. In higher forms the term " skull " is usually applied to both these structures, but it should be realised that they are fundamentally distinct. Petromyzon has no biting jaws ; instead, its mouth is round, for which reason the group to which it belongs is known as the Cyclostomes. The splanchnocranium of the Cyclostome is unimportant from the present point of view, because it is so much specialised that it can throw little light on the skulls of higher forms.

The fins are supported by rays of cartilage.

Alimentary System.—In order to understand the structure of the alimentary canal and associated organs more easily, it is necessary to leave the adult Petromyzon and to turn to its larval form, which is known as the Ammocœte. The mouth is situated in a buccal cavity separated from the pharynx by a velum. The side walls of the pharynx are pierced by seven pairs of gill-slits.

Along the floor of the pharynx runs a groove which is continuous anteriorly with a pair of peripharyngeal bands. These rise up on each side of the mouth, behind the velum. Posteriorly the groove runs into a ventral hollow downgrowth of the

pharynx. The floor of this downgrowth is folded and contains four rows of glandular cells. It is obvious that this structure is practically identical with that of the endostyle of Amphioxus. Behind the pharynx, the gut leads straight back through an intestine to the anus.

During the metamorphosis from the Ammocœte larva to the adult, certain important changes take place. The buccal cavity develops into a sucker with horny teeth, and the rasping tongue is formed in the floor of the pharynx. The endostyle closes up and its glandular and ciliated cells disappear but
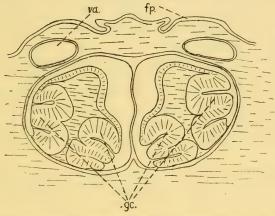
FIG. 16.—Petromyzon : transverse section through the endostyle of an Ammocœte larva.

gc, the four tracts of glandular cells ; *fp*, floor of the pharynx ; *va*, branch of the ventral aorta. (Compare with Amphioxus.)

its duct gives rise to the thyroid gland. From its habit of adhering closely to its food with its sucking mouth, water cannot easily pass through the animal's mouth to its gills. The latter are modified into pouches which take water in through their external apertures and then expel it again. Inside, the pharynx becomes divided into two parts, one above the other. The upper portion becomes the definitive passage from the mouth to the intestine ; the lower becomes the branchial tube. The latter is blind behind, receives the inner openings of the seven pairs of gill-pouches, and opens

in front into the buccal cavity guarded by the remnants of the velum.

These changes which take place during the life of Petromyzon show that it is a form descended from ancestors which practised the ciliary mode of feeding, since when, it developed a specialised and somewhat degenerate method of feeding of its own.

Behind the pharyngeal region the gut runs straight as the intestine to the anus : there is no indication of a curved and enlarged region known in all higher forms as the stomach. In the intestine the surface of absorption is slightly increased by a small inwardly projecting ridge which, as it winds helicoidally down the intestine, is known as a " spiral valve." The lining of the gut is ciliated.

Ventral outgrowths from the front of the intestine form the liver. It is more or less degenerate in the adult, and it is said that its communication with the intestine by means of the bile-duct becomes lost, so that its only communication is with the blood-vessels. The pancreas is very rudimentary, and represented only by scattered packets of cells along the intestine.

Vascular System.—Running forwards beneath the intestine, and therefore in the splanchnopleur, is a subintestinal vessel. It runs to the liver where it breaks up into capillaries forming a hepatic portal system. From the liver, the vessel proceeds forwards as the hepatic vein, and soon swells out beneath the pharynx and becomes specialised to form a muscular pump : the heart.

The heart is composed of the following structures : a sinus venosus, into which the hepatic and other veins enter ; leading on to a thin-walled auricle and a thick-walled ventricle. The entry to and exit from the ventricle, which does the propelling of the blood, are guarded by valves so that blood cannot flow in the reversed direction. The length of the structures composing the heart is greater than that of the space (pericardium) in which they lie ; consequently the heart is slightly bent on itself into the form of an S.

From the ventricle the ventral aorta runs forward beneath

the branchial duct, and gives off paired afferent branchial vessels to the gill-arches, where they break down into the capillaries of the gills. Paired efferent branchial vessels then gather up the oxygenated blood and lead it to the dorsal aorta, which runs back just beneath the notochord, and is continued forwards into the head as the internal carotid artery.

On each side of the dorsal aorta are paired anterior and posterior cardinal veins which lie of course in the body-wall or somatopleur. At the level of the sinus venosus, the cardinals of each side communicate with the heart by means of the ductus Cuvieri. But as the cardinals are in the body-wall and the sinus venosus is in the gut-wall, the ductus Cuvieri have to cross the cœlom. This they do by means of a bridge of cœlomic epithelium called the transverse septum. The cœlom is thus divided into an anterior region surrounding the heart: the pericardium; and a posterior perivisceral splanchnocœl. This division is incomplete in the Ammo- cœte larva, but complete in the adult. In the adult there are peculiar median ventral veins in connexion with the tongue, and the ductus Cuvieri on the left side disappears.

The blood is red owing to the presence of hæmoglobin in corpuscles. There is no spleen.

Excretory System.—No nephridia are found in any Craniate. The excretory organ is derived from the segmented nephro- tomes, between the myotomes and the lateral plate. Typically, each nephrotome contains a cavity, the nephrocœl, which opens into the splanchnocœl by ciliated funnels (cœlomostomes), one in each segment. The nephrocœls swell out into little cavities known as Bowman's capsules, into each of which a glomerulus projects. Each glomerulus is formed from an arteriole from the dorsal aorta and a venule leading to the posterior cardinal vein of its side. Glomerulus and Bowman's capsule together form what is known as a Malpighian corpuscle. From each capsule, a tubule grows backwards and into the tubule of its next posterior neighbour. A collecting duct is thus formed on each side, and it grows back, meets its fellow in the middle line, and opens behind the anus on a small papilla. This is the typical structure of the vertebrate kidney, and it is to be
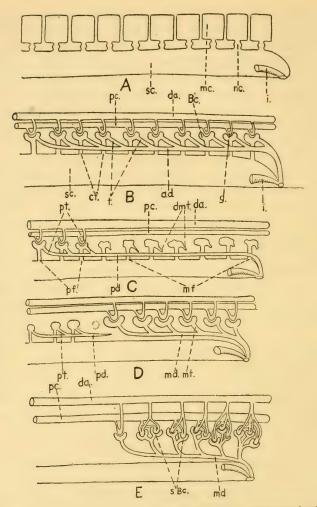
[FIG. 17.—Method of formation of the kidneys in chordate animals.

A, early stage showing the cavity of the splanchnocœl (*sc*) communicating with those of the myocœls (*mc*) by means of the nephrocœls (*nc*).   *i*, intestine. B, hypothetical archinephros. The nephrocœls now known as Bowman's capsules (*Bc*) preserve their connexions with the splanchnocœl by means of ciliated funnels (*cf*). From each capsule a tubule (*t*) grows back and joins that formed from the next posterior capsule to form the archinephric duct (*ad*). With each Bowman's capsule is associated a glomerulus (*g*), formed from an arteriole from the dorsal aorta (*da*) and a

noted that the tubules which form it are of mesodermal origin, coming from the cœlomic epithelium, and are sharply to be distinguished from nephridia, which are ectodermal in origin.

Originally these cœlomostomes must have served to free the genital products (as indeed the spermatozoa are freed in all higher forms), and excretion also took place through them from the cœlom to the exterior. Then the excretory products were brought to the tubules by blood-vessels and the cœlom lost its excretory function. The tubules lose their connexion with the splanchnocœl. In Petromyzon the cœlomostomes were never open. In other forms, the cœlomostomes may persist. In Myxine, a close relative of Petromyzon, the Malpighian corpuscles retain their segmental arrangement, but in all other forms they become increased in number, and the segmental correspondence is lost.

The tubules arise in two sets. First an anterior lot, opening into the pericardium, form the pronephros, and their duct (the pronephric duct) grows right back to the papilla. The pronephros nearly disappears in the adult Petromyzon, and is replaced in function by an identical but more posterior set of tubules which form the mesonephros. The mesonephric tubules grow into the pronephric duct which they find ready-made for them, and which becomes known as the mesonephric duct. The mesonephric tubules develop later than the pronephric tubules, but are of essentially the same nature. This is illustrated in Bdellostoma, another relative of Petromyzon, in which a continuous series of tubules arises, the more anterior of which become the pronephros, and the posterior

venule to the posterior cardinal vein (*pc*). C, condition in most young chordates, in which an anterior set of pronephric tubules (*pt*) gives rise to a pronephric duct (*pd*) before the more posterior mesonephric tubules (*dmt*) are properly formed. *pf*, pronephric funnels ; *mf*, mesonephric funnels. D, condition in older chordates, and retained throughout life in Myxine. The pronephros has degenerated, and the mesonephric tubules (*mt*) have joined the pronephric duct which now bears the name mesonephric duct (*md*). The latter is no longer continuous with the anterior portion of the pronephric duct. The capsules of the mesonephros lose their connexion with the splanchnocœl, but they retain their simple segmental arrangement. E, condition in Petromyzon. The pronephros has degenerated, and the number of capsules in the mesonephros has been increased by the formation of secondary Bowman's capsules (*sBc*).

the mesonephros. Such a primitive kidney approaches very closely to the hypothetical Archinephros, with its archinephric duct. It is important to note that in the Cyclostomes there is but one kidney-duct on each side. The kidneys and their ducts hang down in the cœlom as the so-called nephric fold.

Genital System.—The gonads are situated in a ridge hanging down from the roof of the cœlom. Originally paired, the gonad is single and median in Petromyzon. In both sexes the genital products are shed freely into the splanchnocœl. In front of the place where the two mesonephric ducts join, each
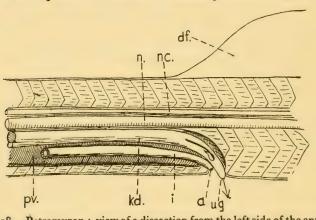
Fig. 18.—Petromyzon : view of a dissection from the left side of the anus (*a*) and urinogenital (*ug*) aperture.

df, dorsal fin ; *i*, intestine ; *kd*, kidney duct ; *n*, notochord ; *nc*, nerve-cord ; *pv*, perivisceral cœlomic cavity. The arrow is passed through the genital pore from the cœlom.

duct has a small pore opening into the splanchnocœl, and it is through these pores that the genital products escape to the exterior ; they have no special ducts.

Cœlom and Mesoderm.—The eventual division of the cœlom by the transverse septum into pericardial and peri-visceral cavities has already been mentioned. The myocœls are completely obliterated, and the only other portions of cœlomic cavity are the kidney-tubules and ducts. The first three somites are drawn off into the service of the eyeballs, and the fourth forms the first proper trunk-muscle. The

series of somites is therefore complete, and no segment has lost its somite. The myotomes are W-shaped, which condition can easily be derived from the V-shaped myotomes of Amphioxus by the turning forwards of their upper and lower ends. They are not subdivided into dorsal and ventral portions as in higher forms.

The characters of Petromyzon and Cyclostomes can be analysed under three headings : those which show an advance from the condition of Amphioxus, those which are primitive when compared with higher forms, and those which are secondary and specialised.

Characters shown by Petromyzon, absent in Amphioxus and typical of Craniata :

> Formation of a distinct head, brain, and skull ;
> Formation of a distinct heart ;
> Formation of pro- and mesonephric kidneys ;
> Epidermis several cells in thickness ;
> Dorsal nerves with ganglia ;
> Rudimentary vertebral column ;
> Myotomes W-shaped ;
> Rudimentary sympathetic nervous system.

Characters shown by Petromyzon (and Cyclostomes) which are primitive when compared with higher forms :

> Endostyle, ciliated groove and velum of the Ammocœte larva ;
> Emergence of glossopharyngeal behind the cranium ;
> Dorsal and ventral nerves separate and unconnected in each segment ;
> Fourth segment forming a complete myotome : no myotomes lost ;
> Notochord unconstricted by vertebral column ;
> Kidney-tubules segmental in Myxine ;
> Myotomes not divided into dorsal and ventral portions ;
> Persistence (although slight) of the pronephros ;
> Absence of biting jaws ;
> Absence of paired fins ;

Absence of dermal skeleton (fin-rays or teeth) ;
Absence of special stomach ;
Absence of special genital ducts ;
Absence of medullated nerves.

Specialised characters of Petromyzon :

Rasping tongue ;
Sucking mouth ;
Horny teeth ;
Sac-like gill-pouches ;
Separate branchial duct ;
Large hypophysial sac ;
Single median dorsal pore for nasal organs and hypo-
physial sac.

LITERATURE.

GOODRICH, E. S. Vertebrata Craniata, Cyclostomes and Fishes. Black,
London, 1909.

PARKER, T. J. A Course of Instruction in Zootomy (Vertebrata). Mac-
millan, London, 1884.
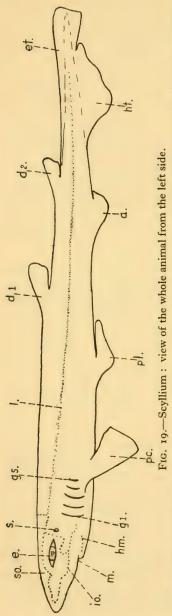
CHAPTER IV

SCYLLIUM, A CHORDATE WITH JAWS, STOMACH, AND FINS

Externals.—The dogfish possesses an elongated body with a distinct head and tail, the latter provided with a tail-fin of which the ventral lobe is larger than the dorsal (heterocercal). There are two median dorsal fins. The most obvious advance over the Cyclostome condition is the possession of paired fins, of which there are two pairs : a pectoral and a pelvic.

The head has paired nasal sacs and eyes. The mouth is situated some distance behind the anterior end of the snout. Behind the mouth on each side are six openings into the pharynx. The first pair of these is small and more dorsally situated than the others ; it is the spiracle. The remaining five are the gill-slits, numbered 1 to 5. The anus lies in a cloaca (joint opening of the alimentary and urino-genital systems) in the midventral line behind the pelvic fins, and on each side of it is a small pore (the so-called abdominal pore) communicating with the cœlom. In the male, there is a pair of claspers on each side of the cloaca.

Denticles.—The body is covered all over with small sharp spikes, with the points directed backwards. These are the placoid scales or denticles. They are made of dentine covered over with a cap of enamel. Dentine is a hard substance produced by mesodermal cells beneath the epidermis ; and it is identical with the substance of which the teeth of all vertebrates are made. It consists of a calcified ground-substance in which filamentous processes of cells are to be found, but no cells themselves. In this particular it differs from bone. The enamel is formed from the ectoderm. On the inner rim of the jaws just inside the mouth, denticles are also found. They

37

FIG. 19.—Scyllium: view of the whole animal from the left side.

a, anal fin; d1, d2, first and second dorsal fins; e, eye; et, epicaudal (dorsal) lobe of heterocercal tail-fin; g1, g5, first and fifth gill-slits; hm, hyomandibular lateral-line canal; ht, hypocaudal (ventral) lobe of tail-fin; io, infraorbital lateral-line canal; l, lateral-line canal; m, mouth; pc, pectoral fin; pl, pelvic fin; s, spiracle; so, supraorbital lateral-line canal.

get pushed out to the edge of the jaws, and act as biting teeth. When worn out, they are replaced by others which are pushed up in their turn to the biting edge (see Fig. 122, p. 263).

Lateral Line.—In various places over the body, there are peculiar organs belonging to what is known as the lateral-line system. Essentially, they take the form of canals sunk beneath the skin, and opening to the exterior at intervals. In these canals are sense-organs whose probable function it is to appreciate low-frequency vibrations in the water. One of these canals runs along the side of the body from the tail to the head, and is the true " lateral-line canal." At about the level of the first gill-slit, it gives off a transverse occipital canal which runs over the top of the head and meets its fellow from the opposite side. It continues forwards over the spiracle as a short temporal or postorbital canal, and divides into two. One

portion goes forwards over the eye as the supraorbital canal, the other beneath it as the infraorbital canal. In addition there is typically a canal which runs down behind the spiracle (hyomandibular canal) to the lower jaw (mandibular canal); but these two are more or less interrupted in the dogfish.

Close to the lateral-line canals in various places there are little pits leading from pores on the surface down narrow tubes to ampullæ at the bottom, where there are sense-organs. These
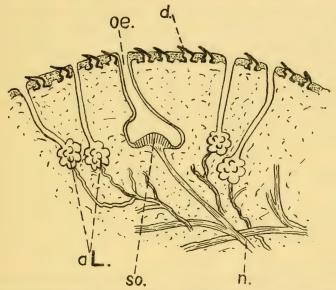
FIG. 20.—Scyllium: section through the skin showing the ampullæ of Lorenzini (aL), denticles (d), nerve-fibres (n), opening of a lateral-line canal (oe), and a sense-organ (so) in the canal.

are the pit-organs, or ampullæ of Lorenzini. Together with the lateral-line system they constitute the neuromast, or acustico-lateralis organs, to which the ear also belongs. These organs are also present in Petromyzon, but not so definitely arranged.

Ear.—The ear consists of a pit sunk in from the skin and forming a sac, which communicates with the exterior by a long tube and a fine pore; the ductus endolymphaticus. The sac is divided into a more dorsal utricle, and a more ventral saccule.

The utricle bears three semicircular canals, at the base of each of which is a swelling or ampulla containing an organ of balance. The whole ear is to be regarded as a very much enlarged lateral-line organ.

Eye.—The eyes are hollow cups with sensitive retinal layer, iris, pigment layer, vascular choroid, and protective cartilaginous sclerotic. Fitting into the aperture of the eye-
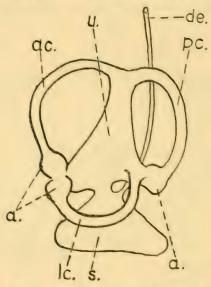
FIG. 21.—Scyllium : view of the outer side of the left auditory sac. *a*, ampulla ; *ac, lc*, and *pc*, anterior, lateral, and posterior semicircular canals ; *de*, ductus endolymphaticus ; *s*, saccule ; *u*, utricle.

cup is the spherical lens, which is attached to the cup by a ventral ciliary muscle.

The movements of the eyeball are effected by six muscles. Four of these (superior, internal, inferior, and external rectus muscles) exert straight pulls on the four cardinal points of the eyeball, and turn it upwards, forwards, downwards, or backwards respectively. The two others (superior and inferior oblique muscles) pull it obliquely either forwards and upwards or forwards and downwards.

Nose.—The nose is formed by a pair of pits on each side

of the under surface of the snout just in front of the mouth, and connected with it by grooves which run to its corners. Inside the pits, the sensory olfactory epithelium is thrown into a number of folds.

Nervous System.—As in the Cyclostome, the brain is divisible into fore-, mid-, and hind-regions. Further, the fore- and hind-brains can also be divided into two for facilitating description. There are therefore five sections of the brain, whose names from front to rear are : telencephalon, diencephalon (also called thalamencephalon), mesencephalon, metencephalon, and myelencephalon. The first two divisions together form the forebrain or prosencephalon, the last two form the hindbrain or rhombencephalon. The sides of the telencephalon (or end-brain) are greatly expanded, and bear the olfactory bulbs. On the floor is the optic chiasma, where the optic nerves cross over from one side to the other. In front of this is the lamina terminalis ; the thickened lower portions of the side walls are the corpora striata.

A transverse fold in the roof, the velum transversum, marks the beginning of the diencephalon (or between-brain). The sides are thickened and known as the optic thalami, the floor is depressed to form the infundibulum to which the pituitary is attached. The roof bears a projection : the epiphysis, vestige of the pineal eye.

The floor, sides, and roof of the mesencephalon are thickened, so that its cavity is reduced and is known as the aqueduct of Sylvius. The roof forms the paired optic lobes.

The roof of the metencephalon is thick and forms the cerebellum, that of the myelencephalon is thin. To the sides of and behind the cerebellum are the restiform bodies.

The cavity of the forebrain is called the 3rd ventricle ; that of the hindbrain the 4th ventricle. The brain is surrounded by a membrane carrying blood-vessels (the pia mater), and this dips down in folds from the roof of the 3rd and of the 4th ventricles to form a choroid plexus. Connecting one side of the brain with the other there are tracts of fibres called commissures. Of these, the habenular and the posterior are in the roof of the between-brain and midbrain respectively.

There is also an (anterior) transverse commissure in the lamina terminalis, but on the whole there is little interconnexion between the two sides of the brain.

The myelencephalon, or medulla oblongata, passes back gradually into the spinal cord. This is a tube with thick walls and a small central cavity, continuous of course with that of the brain. The nerve-cells are grouped round the centre of the
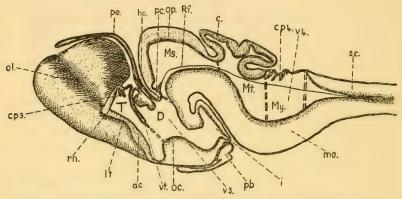
FIG. 22.—Scyllium : median view of a longitudinal section through the brain.

The various regions of the brain are separated by broken lines across the central cavity, and indicated by the letters : *T*, telencephalon (endbrain) ; *D*, diencephalon (or thalamencephalon, between-brain) ; *Ms*, mesencephalon (midbrain) ; *Mt*, metencephalon (anterior part of hindbrain) ; *My*, myelencephalon (posterior part of hindbrain) ; *ac*, anterior commissure ; *c*, cerebellum ; *cp* 3 and 4, choroid plexus of the third and fourth ventricle ; *hc*, habenular commissure ; *i*, infundibulum ; *lt*, lamina terminalis ; *mo*, medulla oblongata ; *oc*, optic chiasma ; *ol*, olfactory lobe ; *op*, optic lobe ; *pb*, pituitary body ; *pc*, posterior commissure ; *pe*, pineal stalk ; *Rf*, Reissner's fibre ; *rn*, recessus neuroporis ; *sc*, spinal cord ; *v* 3 and 4, cavity of the third and fourth ventricle ; *vt*, velum transversum. (Partly after Nicholls.)

cord, and form the " grey matter." Outside them and occupying the remaining space are the ascending and descending tracts of nerve-fibres, provided with medullary sheaths, and forming the " white matter." This arrangement of central grey matter and peripheral white matter holds also in the brain. Only in the cerebellum and in the optic lobes are there some superficial nerve-cells ; *i.e.* grey matter outside white.

Attention may here be called to Reissner's fibre. It is a wire-like structure of unknown function which runs from the posterior commissure in the roof of the midbrain, through the cavity of the nerve-tube right down to its hind end where it is attached. Reissner's fibre is present in most chordates, but not in Amphioxus nor in man.

The pia mater has already been mentioned. It encircles
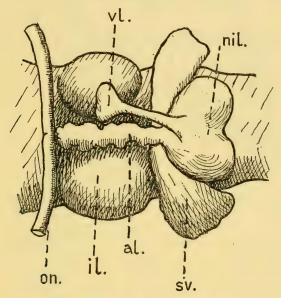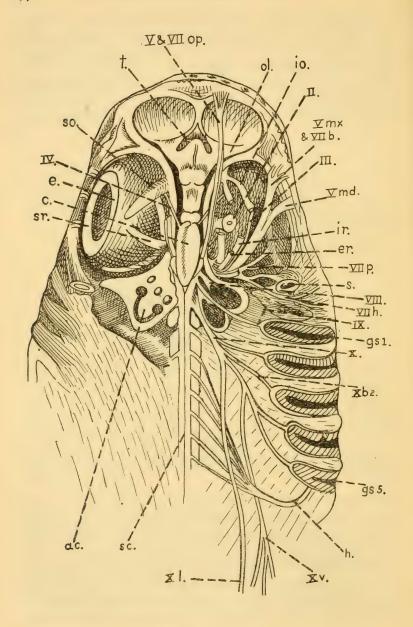
FIG. 23.—Scyllium : ventral view of the brain showing the pituitary body.

al, anterior lobe ; *nil*, neuro-intermediate lobe ; *vl*, ventral lobe of the pituitary body ; *il*, floor of the diencephalon ; *on*, optic nerve ; *sv*, saccus vasculosus.

the whole nerve-tube, and corresponds to the choroid layer of the eye. Outside it is a tougher membrane, the dura mater, protective in function. It is applied to the inner wall of the skull and corresponds to the sclerotic layer of the eye.

Spinal Nerves.—In each segment on each side, behind the head, the spinal cord gives off a ventral nerve, and a dorsal nerve with a ganglion on it. These two nerves join to form a mixed spinal nerve. Soon after joining, their components

separate out again to their various destinations. The ventral roots are distributed to the muscles of the myotomes along the trunk and in the fins, the dorsal roots to the sense-organs. In addition, each spinal nerve sends a branch to the sympathetic ganglia, which are joined to one another by nerve-fibres which form two longitudinal chains, one on each side of the dorsal aorta.

The nerve-fibres are medullated, except those of the sympathetic system.

Cranial Nerves and Head-Segmentation.—The cranial nerves are of importance in unravelling the segmentation of the head. Some of them are dorsal roots, and some are ventral, but they never join to form mixed nerves as in the region of the trunk.

The olfactory nerve (No. I) is not a true nerve like the others, for it is formed of the fibres produced by the cells of the nasal epithelium which grow in to the forebrain (in the manner characteristic of all the nerves in Amphioxus). The small nervus terminalis which accompanies it for some distance is also devoid of segmental significance.

Similarly the optic nerve (No. II) is not segmental, for the whole optic cup and stalk are really parts of the brain itself.

The dorsal root of the first (or premandibular) segment is the profundus (No. V 1), which unfortunately disappears in Scyllium. In the closely related Squalus it is present, and runs forwards through the socket for the eye (the orbit) under the superior oblique muscle, and innervates the skin of the snout.

Fig. 24.—Scyllium : dorsal view of a dissection of the cranial nerves, from a drawing by Mr. B. W. Tucker.

II, optic ; III, oculomotor ; IV, trochlear ; V *md*, mandibular branch of trigeminal ; V and VII *op*, superficial ophthalmic branches of trigeminal and facial ; V *mx* and VII *b*, maxillary branch of trigeminal and buccal branch of facial ; VII *p*, palatine branch of facial ; VII *h*, hyomandibular branch of facial ; VIII, auditory ; IX, glossopharyngeal ; X, vagus ; X *b* 2, second branchial branch of vagus ; X *l*, lateral-line branch of vagus ; X *v*, visceral branch of vagus ; *ac*, auditory capsule ; *c*, cerebellum ; *e*, eye ; *er*, external rectus eye-muscle ; *gs* 1 and 5, first and fifth gill-slits ; *h*, hypoglossal nerve ; *io*, inferior oblique eye-muscle ; *ir*, inferior rectus eye-muscle ; *ol*, olfactory lobe ; *s*, spiracle ; *sc*, spinal cord ; *so*, superior oblique eye-muscle ; *sr*, superior rectus eye-muscle ; *t*, terminalis nerve.

The corresponding ventral root of the first segment is the oculomotor (No. III), which supplies the following four eye-muscles : superior, internal, and inferior rectus, and the inferior oblique. It is also connected with the sympathetic ciliary ganglion.

The second or mandibular segment has as its dorsal root the trigeminal (No. V, 2 and 3). This nerve is composed of a superficial ophthalmic branch running forwards over the eye, a maxillary branch in the upper jaw and a mandibular branch in the lower jaw. These nerves are distributed to sense-organs in the skin, and also to the muscles which move the jaws.

The corresponding ventral root of the second segment is the trochlear (also called pathetic ; No. IV), which innervates the superior oblique eye-muscle.

The dorsal root of the third or hyoid segment is the facial nerve (No. VII). It is made up of the following branches :—

> superficial ophthalmic, running forwards over the eye in company with that of the trigeminal, and innervating the supraorbital lateral-line organs ;
>
> buccal, running forwards beneath the eye and innervating the infraorbital lateral-line organs ;
>
> hyomandibular, passing down behind the spiracle to innervate the lateral-line organs of the lower jaw, and the muscles of the hyoid arch ;
>
> palatine, innervating the taste-organs on the roof of the mouth ;
>
> pretrematic, running down in front of the spiracle, innervating sense-organs.

The auditory nerve (No. VIII), which innervates the sense-organs of the ear, is really an enlarged and specialised branch of the facial nerve.

The corresponding ventral root of the third segment is the abducens (No. VI), which supplies the external rectus eye-muscle.

The dorsal root of the fourth segment is the glossopharyn-geal (No. IX). It has a branch to the temporal region of the

lateral-line canal, a pharyngeal branch to the gut, and a branchial branch which divides ; a small branch running in the hyoid arch in front of the first gill-slit, and the main branch running behind the 1st gill-slit in the 1st branchial arch. The glossopharyngeal thus bears the same relations to the 1st gill-slit as the facial does to the spiracle.

There is no ventral root to the fourth segment ; the somite which it would innervate disappears.

The fifth segment has also lost its myotome and ventral root during development. To each of the remaining gill-slits, 2nd to 5th, there corresponds a branchial nerve, the main branches running behind the slits and pretrematic branches in front of them. These nerves are the dorsal roots of the fifth, sixth, seventh, and eighth segments, which have joined together to form the vagus (No. X). The lateral-line organs in the occipital region of the head and all along the side of the trunk to the tail, are innervated by branches of the vagus. In addition, the vagus sends a visceral branch to the heart and stomach, forming part of the parasympathetic system.

The ventral roots of the sixth and following segments innervate the myotomes of their segments, and also contribute to a nerve—the hypoglossal—which runs back over the gill-slits, down behind them and forwards beneath them to innervate some muscles under the pharynx.

The ninth is the first segment to have a fully formed mixed spinal nerve.

Skull.—The skull and all the skeleton is made of cartilage.

The glossopharyngeal and vagus nerves emerge well in front of the hind end of the skull. The latter therefore occupies a larger number of segments than in Petromyzon, namely seven. The skull encloses the brain completely except for an aperture in its roof. The cranial nerves all emerge through special holes or foramina. The auditory and olfactory capsules are firmly fused on. The notochord disappears in the skull-region, and a definite joint is formed between the hind end of the skull and the front of the vertebral column.

The jaws are formed by the skeleton of the first or mandibular visceral arch, which separates the mouth from the

spiracle. The upper and lower portions of this arch's skeleton move on one another and form the upper and lower jaws. The skeleton of the upper jaw is the pterygo-quadrate, that of the lower is Meckel's cartilage. The possession of jaws is the criterion of the group Gnathostomata, to which Scyllium and all higher forms belong. The arches between the gill-slits also have cartilaginous rods. That of the second or hyoid
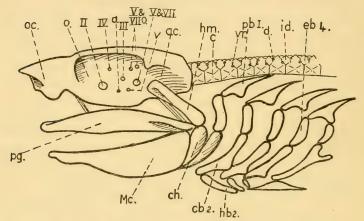
FIG. 25.—Scyllium : view of skull and visceral arches.

a, foramen for efferent pseudobranchial artery ; *ac*, auditory capsule ; *c*, centrum of vertebra ; *ch*, ceratohyal ; *cb* 2, ceratobranchial of second arch ; *d*, foramen for dorsal spinal nerve-root ; *eb* 4, epibranchial of fourth arch ; *hb* 2, hypobranchial of second arch ; *hm*, hyomandibula ; *id*, inter-dorsal cartilage ; *Mc*, Meckel's cartilage ; *o*, orbit ; *oc*, olfactory capsule ; *pb* 1, pharyngobranchial of first arch ; *pg*, pterygoquadrate cartilage ; *v*, foramen for pituitary vein ; *vr*, foramen for ventral spinal nerve-root ; II, optic nerve foramen ; III, oculomotor nerve foramen ; IV, trochlear nerve foramen ; V and VII, trigeminal and facial foramen ; V and VII *o*, foramina for ophthalmic branches of trigeminal and facial.

visceral arch (separating the spiracle from the 1st gill-slit) is composed of a dorsal portion, the hyomandibula ; and a ventral portion, the ceratohyal, and basihyal. The following visceral arches are made up of four pieces on each side, which are from above downwards, the pharyngobranchial, epi-, cerato-, and hypobranchial. There is also a median basi-branchial. The pterygo-quadrate and the hyomandibula represent the " epi " elements of their respective arches,

Meckel's cartilage and ceratohyal the " cerato " elements. There is no difficulty in recognising the fact that the jaws are simply slightly modified visceral arches. These cartilaginous arches lie in the splanchnopleur. Stiffening the partitions between the gill-slits are extrabranchials and branchial rays.

It is important to notice that these jaws and branchial arches, which together constitute the splanchnocranium, are not fused on to the neurocranium or attached to it otherwise than by ligaments.

The pterygo-quadrate is slung from the skull by the hyomandibula, the upper end of which is attached to the auditory capsule. This method of suspension of the upper jaw is called hyostylic. The upper jaw does not touch the neurocranium itself. In addition to its attachment by the hyomandibula, there are two ligaments, the ethmoid and the postspiracular, which tie the upper jaw to the brain-case.

The ordinal numbers by which the arches, segments, and slits are known are unfortunately liable to lead to confusion, for which reason they are tabulated below :

Segments.	Arches or Bars.	Slits or Clefts.
1st = premandibular		
2nd = mandibular	1st visceral = mandibular	
		1st visceral = spiracle
3rd = hyoid	2nd visceral = hyoid	
		2nd visceral = 1st gill slit
4th	3rd visceral = 1st branchial	
		3rd visceral = 2nd gill slit
5th	4th visceral = 2nd branchial	
		4th visceral = 3rd gill slit
6th	5th visceral = 3rd branchial	
		5th visceral = 4th gill slit
7th	6th visceral = 4th branchial	
		6th visceral = 5th gill slit
8th	7th visceral = 5th branchial	

Vertebral Column.—Corresponding to each septum between two segments, there are paired basidorsal and basiventral cartilages, surrounding the notochord. The sheath of the notochord is penetrated by these cartilages which, together, form a bobbin-like ring or centrum, which constricts and interrupts the notochord. The centra articulate on one another end to end, and in this way a vertebral column is

E

formed. Rising up from the centra are the neural arches, which enclose the spinal cord in a canal. Alternating with these are interdorsal cartilages. The ventral nerves emerge behind the neural arches, and the dorsal roots behind the
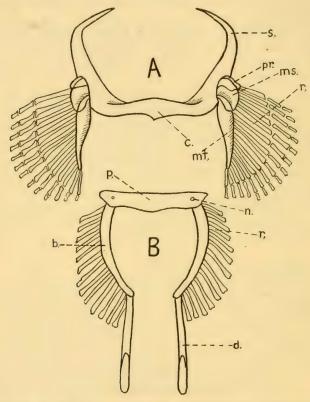
FIG. 26.—Scyllium : ventral view of, A, pectoral, and B, pelvic girdle.

b, basipterygium ; *c*, coracoid region ; *d*, skeleton of clasper (present in the male) ; *ms*, mesopterygium ; *mt*, metapterygium ; *n*, nerve foramen ; *p*, pelvic cartilage ; *pr*, propterygium ; *r*, radials ; *s*, scapular region.

interdorsal cartilages. Ventral extensions of the basiventrals beneath the centra in the tail-region form hæmal arches, in which blood-vessels run. Lateral extensions of the basiventrals give rise to the ribs. They extend in the septum

that divides the myotomes horizontally, and are called " dorsal " ribs (see p. 307).

Fins.—The median fins are supported by jointed cartilaginous rods or radials. These were originally direct continuations of the neural and hæmal arches, but as a result of the shortening of the bases of the fins (or concentration), the radials no longer correspond with the vertebræ, except in the ventral lobe of the tail. In addition to the cartilaginous radials, the web of the fin is supported by horny dermal finrays, close under the skin on each side of the radials. These rays, or ceratotrichia, are more numerous than the radials.
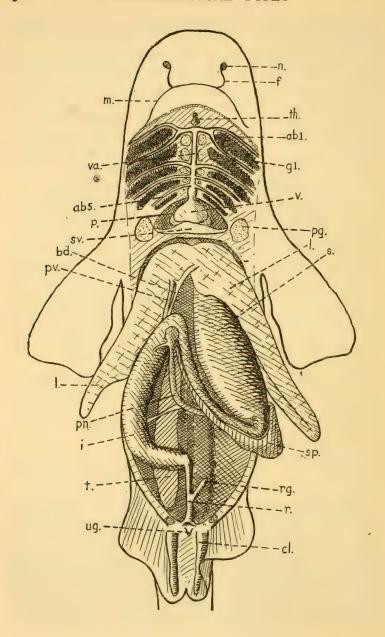
The paired fins also have an internal skeleton of cartilaginous radials, and are anchored to the body by girdles lying in the body-wall. The pectoral girdle is a half-hoop of cartilage set transversely to the long axis of the body, with the free ends pointing upwards. On each side is a hollow, the glenoid cavity, into which the cartilages of the fins fit. The latter cartilages are the most proximal radials, which form three large cartilages, the pro-, meso-, and metapterygia. The ventral portion of the pectoral girdle is termed the coracoid region ; from the glenoid cavity to the free tips which project dorsally, the cartilage is known as the scapular region.

The pelvic girdle is formed by a transverse cartilage, at each end of which an elongated backwardly-directed basipterygium is articulated. This basipterygium forms the axis of the pelvic fin, and bears a number of cartilaginous radials on its anterior border.

The pectoral and pelvic fins, as well as the median fins, have their webs supported by horny dermal fin-rays, the ceratotrichia.

Alimentary System.—The mouth leads into the pharynx, the sides of which are pierced by the spiracle and the gill-slits. The food consists of fair-sized pieces of prey, seized by the jaws, and in no danger of being lost through the gill-slits. Behind the pharynx is the œsophagus which leads into a large stomach. In its formation, the gut has been kinked to the left, so that the stomach is a well-defined region. Ventral to it is a large liver with a gall-bladder from which a bile-duct leads

to the intestine. In the U-shaped bend which the stomach makes with the intestine lies the pancreas, the duct from which enters the intestine close to the bile-duct. The intestine bends backwards and runs straight to the rectum, which has a small diverticulum (the rectal gland), and leads to the cloaca. The gut is considerably longer than the distance from the mouth to the cloaca, and the "slack" is accounted for by the asymmetry of the stomach. This asymmetry persists through all the higher vertebrates. The internal surface of the intestine is increased by a fold forming the spiral valve.

Cœlom and Myotomes.—The gut is suspended in the splanchnocœl by a dorsal mesentery. Anteriorly the splanchnocœl is almost completely cut off from the cavity of the pericardium by the transverse septum, which leaves only small pericardio-peritoneal canals. Posteriorly, the splanchnocœl is in communication with the exterior by the pair of abdominal pores.

The series of somites is not complete. The first three give rise to the eye-muscles, but the myotomes of the fourth and fifth segments disappear during development, leaving the sixth to form the first complete myotome. Each myotome is divided into a dorsal and a ventral portion by a horizontal septum. Into this septum the ribs (known as dorsal ribs) extend. The ventral portions of the most anterior myotomes send muscles forwards beneath the pharynx, in the midventral line. These hypoglossal muscles lose connexion with their original myotomes, and connect the ventral ends of the skeleton of the visceral arches with the coracoid region of the pectoral girdle. The fins contain muscles attached to the radials. These muscles are derived from the myotomes. All muscles

FIG. 28.—Structure and relations of kidneys and ducts in Gnathostomes.
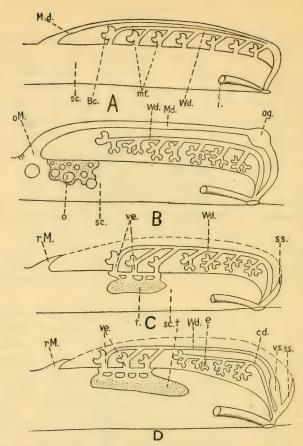
A, larval condition with a Müllerian duct (*Md*) as well as a Wolffian duct (*Wd*). The Bowman's capsules (*Bc*) of the mesonephros communicate with the splanchnocœl (*sc*) through the mesonephric funnels (*mf*). *i*, intestine. B, condition in the adult female. The Müllerian duct persists and functions as an oviduct. The eggs freed from the ovary (*o*) enter the mouth of the oviduct (*oM*), and go down it, past the oviducal gland (*og*) where the shell is secreted. The Wolffian duct is purely excretory in function. C, typical condition of the adult male. The Müllerian duct has disappeared except for vestiges of its opening (*rM*), and the sperm-sac (*ss*). Sperms pass from the testis (*t*) through the vasa efferentia (*ve*) corresponding to mesonephric funnels, to the Wolffian duct. The latter is not only excretory but also genital in function, and is also called the vas deferens. D, condition of the adult male Scyllium. The Wolffian duct connects as usual with the anterior mesonephric tubules and vasa efferentia, but the more posterior part of the mesonephros (*e*) is solely excretory in function; its tubules run into a collecting duct (*cd*) which has separated off from the Wolffian duct. The base of the latter or vas deferens is thickened to form the vesicula seminalis (*vs*), and it and the collecting duct open into the sperm-sac.

derived from myotomes are striated, voluntary, and innervated by ventral nerve-roots. The muscles of the jaws and branchial arches, although visceral, are striated and voluntary ; they are, however, not innervated by ventral roots, but are supplied by dorsal cranial nerves. The remainder of the visceral muscles are all smooth and involuntary, and are to be found in the walls of the gut, blood-vessels, and oviducts. They are innervated by the autonomic system (sympathetic and parasympathetic).

Urino-genital System.—The kidney of the adult dogfish is a mesonephros, similar to that of Petromyzon. Here, however, the excretory and genital systems are closely associated, and it is necessary to treat them together. In Scyllium and all Gnathostomes, in place of the single mesonephric duct on each side, there are typically two. One of these, the Wolffian duct, can be regarded as the original mesonephric duct, and it continues to receive the tubules from the Bowman's capsules. The other is the Müllerian duct which opens into the cœlom by the conjoined openings of the degenerated pronephric tubules, and leads straight back to the cloaca without any connexion with the mesonephric tubules. The degree of development which these ducts show depends on the sex of the animal.

In the male, the testes are paired, and are connected by their anterior ends to the mesonephric tubules by means of the vasa efferentia. These correspond to the original cœlomostomes. Through them the sperms reach the Wolffian duct, which becomes known as the vas deferens ; its posterior end swells to form the seminal vesicle. The anterior portion of the mesonephros therefore is concerned with the evacuation of the genital products in the male. The posterior portion (sometimes and incorrectly called the metanephros) is solely excretory in function. Its tubules run into a collecting duct which connects with the Wolffian duct, both running into a sperm-sac. The two sperm-sacs, one on each side, join to form a urino-genital sinus which opens into the cloaca by a urino-genital papilla. The Müllerian ducts in the male are reduced to a pair of funnels on the ventral side of the œsophagus, and the sperm-sacs.

In the female the mesonephros is entirely excretory in function. The Wolffian ducts are swollen posteriorly to form urinary sinuses which open to the cloaca by a urinary papilla.
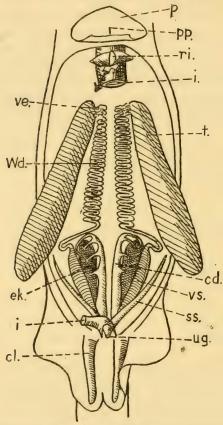
FIG. 29.—Scyllium : ventral view of a dissection of the urinogenital system of a male adult.

cd, collecting duct ; *cl*, clasper ; *ek*, excretory portion of the mesonephros ; *i*, alimentary canal cut ; *p*, pericardium ; *pp*, pericardio-peritoneal canal indicated by an arrow ; *ri*, rudimentary opening of the Müllerian ducts ; *ss*, sperm-sac ; *t*, testis ; *ug*, urinogenital papilla ; *ve*, vasa efferentia ; *vs*, vesicula seminalis ; *Wd*, Wolffian duct or vas deferens.

The right ovary hangs in the cœlom covered by a fold of cœlomic epithelium ; the left ovary disappears. The large eggs when they are ripe drop free into the cœlom. They enter

the funnel-shaped openings of the Müllerian ducts on the ventral side of the œsophagus, and pass down them. These
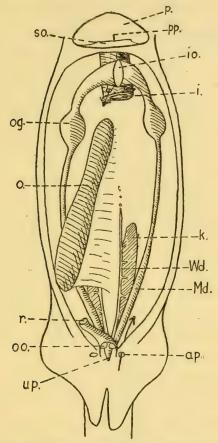
FIG. 30.—Scyllium : ventral view of a dissection of the urinogenital system of a female adult.

ab, abdominal pore through which an arrow is passed ; *i*, œsophagus ; *io*, internal opening of the Müllerian ducts ; *k*, mesonephros ; *Md*, Müllerian duct ; *o*, ovary ; *og*, oviducal gland ; *oo*, opening of Müllerian duct into the cloaca ; *p*, pericardium ; *pp*, pericardio-peritoneal canal through which an arrow is passed ; *r*, rectum ; *so*, sinus venosus cut ; *up*, urinary papilla ; *Wd*, Wolffian duct.

ducts or oviducts swell out into the oviducal glands, where the horny egg-case is secreted, and open separately into the cloaca.

The Müllerian duct is always genital, the Wolffian duct is always excretory, but in the male it is genital in function as well. In some dogfish the mesonephric tubules retain their funnels, opening into the splanchnocœl.

Vascular System.—The vascular system is built on the same plan as that of Petromyzon. The subintestinal vein, which forms the hepatic portal vein, runs to the liver in a portion of mesentery in company with the bile-duct. The veins in the body-wall (or somatic veins) consist of a pair of cardinal veins running parallel with and on each side of the dorsal aorta. They connect with the sinus venosus of the heart by the ductus Cuvieri, which cross the cœlom from the body-wall to the gut-wall, in the transverse septum. The anterior cardinals bring the blood back from the head (orbital sinus and jugular), and from the ductus Cuvieri backwards the veins are known as posterior cardinals. In addition there are paired inferior jugular sinuses bringing blood back from the ventral regions of the head, and paired lateral abdominal veins draining the ventral posterior regions of the body-wall. All these lead into the ductus Cuvieri. The hyoid sinus is in the hyoid arch.

The heart in its pericardium is bent on itself, and is in the form of an S. The sinus venosus, which receives the ductus Cuvieri and the hepatic sinus from the liver, opens into the auricle whence the blood passes through an opening guarded by valves to the thick-walled ventricle. This lies beneath and behind the auricle. In front of the ventricle is a muscular conus arteriosus with two rows of valves which prevent the blood from flowing back into the ventricle. The conus leads through a bulbus (see p. 330) to the ventral aorta from which five pairs of afferent branchial arteries are given off. These break down into the capillaries of the gill-lamellæ in the hyoid and four branchial arches. Each set of lamellæ on one wall of a slit is called a demibranch. There are two demibranchs in each gill-slit except the last, which has only an anterior one.

The oxygenated blood is collected up into four efferent branchial arteries which correspond to gill-slits 1 to 4. They lead to the median dorsal aorta. Each efferent branchial artery is made up of two collecting vessels one on each side of a
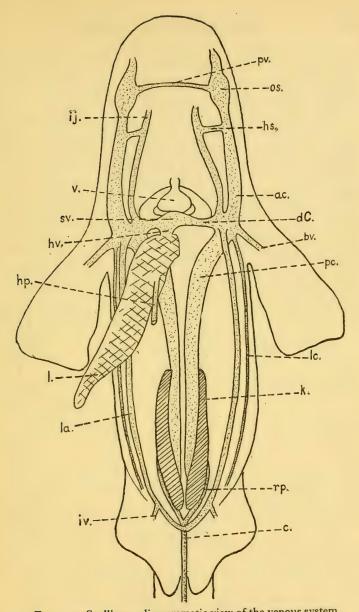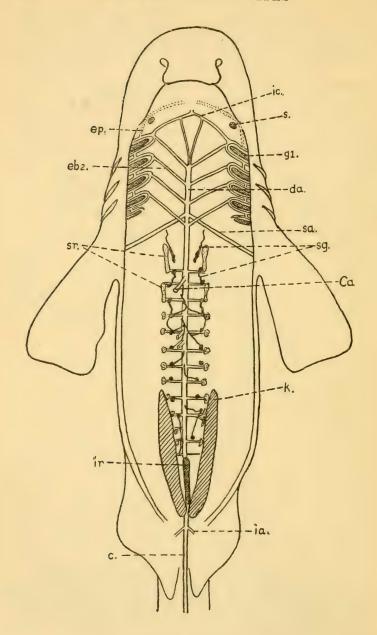
FIG. 31.—Scyllium ; diagrammatic view of the venous system.

ac, anterior cardinal ; *bv*, brachial vein ; *c*, caudal vein ; *dC*, ductus Cuvieri ; *hp*, hepatic portal vein ; *hs*, hyoid sinus ; *hv*, hepatic vein ; *ij*, inferior jugular sinus ; *iv*, iliac vein ; *k*, mesonephric kidney ; *l*, liver ; *la*, lateral abdominal vein ; *lc*, lateral cutaneous vein ; *os*, orbital sinus ; *pc*, posterior cardinal ; *pv*, pituitary vein ; *rp*, renal portal vein ; *sv*, sinus venosus ; *v*, ventricle of the heart.

gill-slit and joining above it. Each gill-arch therefore contains two such vessels and one afferent vessel. The demibranch of the 5th gill-slit is drained by the 4th efferent branchial artery. The demibranch of the spiracle receives already oxygenated blood from the anterior demibranch of the 1st gill-slit. Since it does not oxygenate this blood itself it is called a pseudobranch. The vessel leading from it to the internal carotid inside the skull is the efferent pseudobranchial artery, which can be seen at the back of the orbit or eye-socket.

The anterior prolongation of the dorsal aorta is the internal carotid artery which pierces the base of the skull and supplies the brain. The dorsal aorta gives off paired subclavian arteries to the pectoral fins. Into the mesentery suspending the gut it sends the following: cœliac, lieno-gastric, anterior and posterior mesenteric arteries, which between them vascularise the stomach, liver, intestine, and the well-developed spleen. Farther back the dorsal aorta gives off pelvic arteries to the pelvic fins and renal arteries to the kidneys as well as branches to the gonads, and continues into the tail as the caudal artery. The blood from the tail is returned forwards by the caudal vein which forks, one branch going to each kidney as the renal portal vein. From there the blood is removed by the posterior cardinals.

Ductless Glands (see Chapter XXXIII).—The spleen has already been mentioned; it lies in the mesentery near the stomach (see p. 152).

With the development of jaws, the ciliary mode of feeding has been abandoned. The wheel-organ of Amphioxus is represented by an ectodermal ingrowth—the hypophysis, which comes into intimate contact with the infundibulum of the brain to form the pituitary body.

Fig. 32.—Scyllium: diagrammatic view of the arterial system, and of the sympathetic, supra-renals, and inter-renal (female specimen). Partly from a drawing by Mr. J. Z. Young.

c, caudal artery; Ca, cœliac artery; da, dorsal aorta; eb 2, second efferent branchial artery; ep, efferent pseudobranchial artery; g1, first gill-slit; ia, iliac artery; ic, internal carotid artery; ir, inter-renal body; k, mesonephric kidney; s, spiracle; sa, subclavian artery; sg, sympathetic ganglia, some of which are interconnected by the longitudinal sympathetic nerve-chains; sr, supra-renal bodies.

The endostyle is not present as such, but it has been transformed into the thyroid gland, situated beneath the floor of the pharynx, as in the adult Petromyzon. In some dogfish, its cells still bear cilia.

The lining of the top of the gill-slits grows upwards to form a number of paired glandular masses ; in close association with the anterior cardinal veins they form the thymus glands. Lying on the course of the sympathetic nerve-chains, there are a number of bodies of the same origin and nature as the sympathetic ganglion-cells. They are the supra-renal bodies and originate from the nerve-tube. Posteriorly, between the kidneys is an elongated structure, the inter-renal, which is formed from the cœlomic epithelium. It is interesting to find these two sets of structures separate, for in higher forms they combine to form the adrenals.

Characters present in Scyllium, which are lacking in Petromyzon :

> Biting jaws ;
> Paired fins ;
> Denticles (" placoid scales ") ;
> Dermal fin-rays (ceratotrichia) ;
> Definite stomach and pancreas ;
> Mixed spinal nerves (dorsal and ventral roots joined) ;
> Vertebral column constricting the notochord ;
> Dorsal ribs ;
> Myotomes separated into dorsal and ventral portions ;
> Müllerian and Wolffian ducts ;
> Seven segments included in the skull.

Characters of Scyllium which are primitive when compared with higher forms :

> Absence of bone ;
> Absence of swim-bladder ;
> Gill-slits opening separately to the outside ;
> Heart with single auricle and single ventricle ;
> Separate supra-renals and inter-renals.

LITERATURE

BOURNE, G. C. An Introduction to the Study of the Comparative Anatomy of Animals. Vol. 2. Bell, London, 1915.

CAHN, A. R. The Spiny Dogfish. A Laboratory Guide. Macmillan, New York, 1926.

DANIEL, J. F. The Elasmobranch Fishes. University of California Press, 1922.

GOODRICH, E. S Vertebrata Craniata. Cyclostomes and Fishes. Black, London, 1909.

NICHOLLS, G. F. The Structure and Development of Reissner's Fibre and the Subcommissural Organ. Quarterly Journal of Microscopical Science. Vol. 58. 1913.

CHAPTER V

GADUS, A CHORDATE WITH BONE

Externals.—The genus Gadus includes the cod, whiting, and haddock. In shape, Gadus differs from the dogfish in being relatively shorter and more compressed from side to side. Gadus belongs to the group of higher bony fish known as the Teleostei, and in these the tail is typically forked and outwardly symmetrical, a condition called homocercal. In Gadus the tail is also outwardly symmetrical, but the tail-fin differs from that of other Teleostei. It represents the hind ends of the dorsal and ventral median fins. It is therefore not a homo-cercal but a pseudocaudal fin (see p. 325).
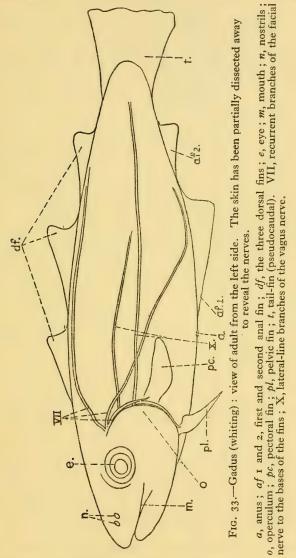
There are three dorsal and two ventral median fins. Of the paired fins the pelvic pair is actually anterior to the pectoral pair in position.

The mouth is bounded by tooth-bearing jaws. On the upper side of the snout, slightly behind the mouth, are the nasal pits. Each of these is a cavity communicating to the exterior by two openings, but not in any way connected with the mouth.

The eyes are large. The gill-slits do not open separately to the exterior, but they are covered over by an operculum. The water which emerges from the gill-slits passes between the hind and lower edges of the operculum and the body. There is no open spiracle. The cloaca is shallowed out, so that the anus and the urino-genital apertures are separate ; the former in front of the latter.

Scales.—Scales form one of the most obvious features of the fish ; they are arranged in W-shaped rows, overlapping from head to tail. Each row primitively corresponds to the

underlying myotome, which is also W-shaped. It is important

FIG. 33.—Gadus (whiting) : view of adult from the left side. The skin has been partially dissected away to reveal the nerves.

a, anus ; *af* 1 and 2, first and second anal fins ; *df*, the three dorsal fins ; *e*, eye ; *m*, mouth ; *n*, nostrils ; *o*, operculum ; *pc*, pectoral fin ; *pl*, pelvic fin ; *t*, tail-fin (pseudocaudal). VII, recurrent branches of the facial nerve to the bases of the fins ; X, lateral-line branches of the vagus nerve.

to notice that the scales are not external, but lie in the meso-dermal tissue (from which they are formed) beneath the

F

epidermis. The scales are thin, flat plates of material akin to bone. They are kept throughout life, and enlarge by concentric additions. These scales have nothing to do with the denticles or placoid " scales " of the dogfish.

Fin-rays.—The fins are supported by fin-rays, but these, instead of being horny and unjointed like the ceratotrichia of the dogfish, are bony and jointed, and are called lepidotrichia. In the more highly-developed bony fish like Gadus, the lepidotrichia correspond in number to the radials of the axial skeleton, in the dorsal and ventral median fins. There is a lepidotrichium on each side of the tip of each radial, and a joint between them enables the web of the fin to be raised or lowered. At the edge of the fin, between the lepidotrichia, there are some small unjointed horny rays called actinotrichia. These correspond to the ceratotrichia of the dogfish.

Skeleton.—The cartilaginous skeleton corresponding to that of the dogfish is present in early stages of development in the bony fish. In the adult, most of this cartilage is replaced by an altogether different skeletal material, viz. bone. Bones which arise in this manner, *i.e.* replacing pre-existent cartilage, are called cartilage-bones or replacing bones. Some bones, on the other hand, have no cartilaginous precursor at all. These arise independently, as more or less flat plates in relation to the surface of the body, though they may sink deeper. These are dermal or membrane-bones. There is no difference in structure between cartilage-bones and membrane-bones, the distinction applies only to the method of origin. Sometimes a bone which develops as a cartilage-bone in one animal may arise as a membrane-bone in another, and vice versa, though these cases are rare. It is to be noted that as a rule a cartilage-bone represents an ossification in a cartilaginous structure which exists in the dogfish, whereas a membrane-bone is a structure which is wholly unrepresented in the dogfish. There is no doubt that the scales, fin-rays, and bones are kindred structures.

Skull.—As in other forms, the skull can be divided into the neurocranium or brain-case, and the splanchnocranium or jaws.
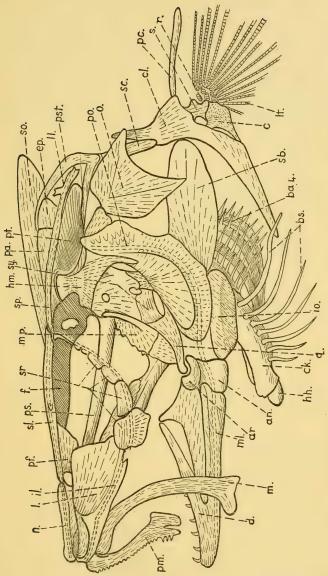
Fig. 34.—Gadus (cod) : skull and pectoral girdle seen from the left side. (*For lettering see p. 70.*)

On the floor of the brain-case are the basioccipital, pre-vomer, and parasphenoid ; in front is the mesethmoid. The roof is formed by the paired nasals, frontals, parietals, and the supraoccipital. The foramen magnum, through which the spinal cord enters the skull, is bounded below by the basi-occipital, above by the supraoccipital, and on each side by the paired exoccipitals.

The auditory capsules are well ossified, and each contains five bones. The lower part of each capsule is made of a prootic
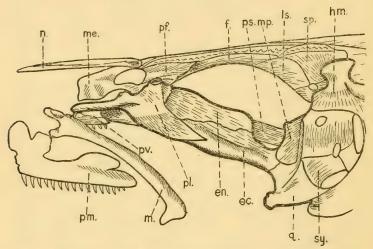
FIG. 35.—Gadus : view of a portion of the skull from the left side, after removal of the lachrymal and suborbital bones, in order to show the palato-pterygo-quadrate arch. (*For lettering see p.* 70.)

in front and an opisthotic behind. Above these are the sphenotic, pterotic, and epiotic bones.

The sides of the brain-case are very incomplete. Anteriorly, there are the paired prefrontals, between the frontal and the parasphenoid on each side. Farther back the paired latero-sphenoids are situated beneath the edge of the frontal and in front of the prootic on each side. A large window is left open in the side of the brain-case, through which many nerves and blood-vessels pass from the skull to the space in which the eye is lodged, called the orbit. Quite at the side there is a string

of little bones which bound the orbit below and behind. These
bones touch the prefrontal anteriorly and the frontal behind.

The most anterior of the
string is the lachrymal,
and the following ones
are the suborbitals and
postorbitals.

Before leaving the
neurocranium, mention
must be made of the
post-temporal, which
touches the epiotic and
pterotic behind. It will
be noticed again in con-
nexion with the shoulder
girdle.

The splanchno-
cranium consists of the
bony supports of the
visceral arches. In the
branchial arches there are
four elements on each
side : pharyngo-, epi-,
cerato-, and hypo-
branchial. The pharyngo-
branchials of the anterior
branchial arches are
fused together ; the
skeleton of the posterior
branchial arches is less
well developed and
ossified. The hypo-
branchials of the anterior
three branchial arches
articulate with a median
and ventral basibranchial. The fused pharyngobranchials
and the ventral elements of the last arch bear teeth.

The skeleton of the first two *visceral* arches (mandibular

Fig. 36.—Gadus : view of the skull from the left side, after removal of the splanchnocranium, in order to show the neurocranium. (*For lettering see p. 70.*)
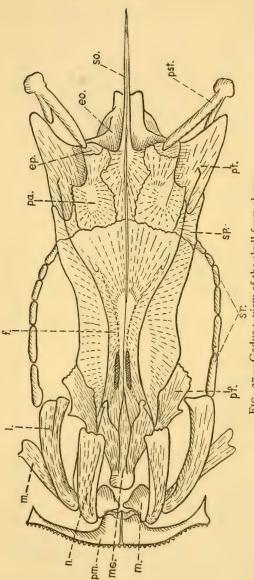
Fig. 37.—Gadus : view of the skull from above.

Explanation of the lettering in Figs. 34 to 37 :

an, angular ; *ar*, articular ; *ba* 4, fourth branchial arch ; *bo*, basioccipital ; *bs*, branchiostegal rays ; *c*, coracoid ; *ck*, ceratohyal ; *cl*, cleithrum ; *d*, dentary ; *ec*, ectopterygoid ; *en*, endopterygoid ; *eo*, exoccipital ; *ep*, epiotic ; *f*, frontal ; *hh*, hypohyal ; *hm*, hyomandibula ; *il*, infraorbital lateral-line canal ; *io*, interopercular ; *l*, lachrymal ; *ll*, lateral-line ossicle ; *ls*, laterosphenoid ; *lt*, lepidotrichia ; *m*, maxilla ; *me*, mesethmoid ; *ml*, mandibular lateral-line canal ; *mp*, metapterygoid ; *n*, nasal ; *o*, opercular ; *oo*, opisthotic ; *pa*, parietal ; *pc*, postcleithrum ; *pf*, prefrontal ; *pl*, palatine ; *pm*, premaxilla ; *po*, preopercular ; *pr*, prootic ; *ps*, parasphenoid ; *pst*, post-temporal ; *pt*, pterotic ; *pv*, prevomer ; *q*, quadrate ; *r*, radials ; *s*, scapula ; *sb*, subopercular ; *sc*, supracleithrum ; *sl*, supraorbital lateral-line canal ; *so*, supra-occipital ; *sp*, sphenotic ; *sr*, suborbitals ; *sy*, symplectic.

and hyoid) is somewhat modified. In the dogfish, the palato-pterygo-quadrate cartilage forms the margin to the upper jaw, but in the bony fish this is no longer the case. Here it is formed by the paired premaxilla and maxilla. Lying median to these are the paired palatine (which touches the brain-case), the three pterygoids (ecto-, endo-, and meta-pterygoid), and, farther back, the quadrate. These bones arise in relation to the palato-quadrate arch, and they therefore no longer form the upper boundary to the mouth, but lie at the sides of its roof. The quadrate articulates with a bone of the lower jaw called the articular, and which corresponds to Meckel's cartilage in the dogfish. Here again a new margin to the jaw is formed, by the dentary. The ventro-posterior part of the lower jaw is formed by the angular.

The suspension of the jaws is hyostylic, *i.e.* the quadrate is connected with the neurocranium by the hyoid arch. The hyoid-arch skeleton consists of an upper hyomandibula which articulates above with the auditory capsule, and is pierced by a foramen for the hyomandibular branch of the facial nerve. Beneath the hyomandibula is the symplectic to which the quadrate is attached. The ventral portion of the arch is made up of the epihyal, ceratohyal, and hypohyal. The epihyal is connected with the symplectic by the interhyal. Below and between the hypohyals is a median basihyal. The ceratohyal bears branchiostegal rays.

The operculum is a posterior extension of the hyoid arch, and it is supported by four bones which are fixed on to the hind edge of the hyomandibula and symplectic. These are the preopercular, opercular, sub-, and interopercular bones.

Pectoral Girdle.—The primitive girdle corresponding to that of the dogfish is formed by a dorsal scapula and a ventral coracoid, on each side. Here they are ossified. With these the pectoral fin articulates by means of the radials. These radials are short and fused, and the web of the fin is supported by the lepidotrichia. Another series of bones is plastered on to this primitive girdle from in front. These bones are the cleithrum, post-cleithrum and supra-cleithrum. The supra-cleithrum articulates with the post-temporal so that the

pectoral girdle is connected with the skull. There is no clavicle, though this bone is present in more primitive bony fish.

Pelvic Girdle.—The pelvic girdle is in the form of a pair of Y-shaped bones lying in the body-wall. The anterior forks of the Y of the bones on each side are joined by a median cartilage. The pelvic fins articulate with the outer side of these bones. The radials in the pelvic fins are even more reduced than those in the pectorals.

Vertebral Column.—The centra of the vertebral column are bony discs, concave on both sides, and the vertebræ articulate with one another by means of facets or zygapophyses. Dorsally, each centrum bears a pair of processes which join to form the neural arch. This arch is produced farther into the neural spine. The radial surmounts this and, in the regions of the dorsal fins, is articulated with the lepidotrichia. The radials scarcely project at all into the fins. The spinal nerves emerge between the neural arches.

In the trunk-region, each centrum bears a pair of ventro-lateral processes, to which the (" ventral," see p. 83) ribs are attached. In the region of the tail these processes are directed downwards, and join to form the hæmal arches. These are prolonged into the hæmal spines, which support the ventral lobe of the tail-fin. The neural arches correspond to basi-dorsals, and the ventro-lateral processes to basiventrals. The notochord is of course obliterated by the centra.

Before leaving the skeleton, it remains to sort out the various bones into cartilage-bones and membrane-bones, and those whose constituents arise in both ways and which may therefore be called mixed bones.

Cartilage-bones.	*Membrane-bones.*	*Mixed bones.*
Neuro-cranium.		
Basioccipital	Nasal	Sphenotic
Exoccipital	Frontal	Pterotic
Supraoccipital	Parietal	Prefrontal
Prootic	Parasphenoid	
Opisthotic	Prevomer	

Cartilage-bones.	*Membrane-bones.*	*Mixed bones.*

Neuro-cranium.

Epiotic (a tendon-bone)	Lachrymal	
Mesethmoid	Suborbitals	
Laterosphenoid	Postorbitals	
Basisphenoid : not always present		

Splanchno-cranium.

Quadrate	Endopterygoid	Palatine
Metapterygoid	Ectopterygoid	
Articular	Premaxilla	
Hyomandibula	Maxilla	
Symplectic	Dentary	
Epihyal	Angular	
Ceratohyal	Opercular	
Hypohyal	Preopercular	
Interhyal	Subopercular	
Basihyal	Interopercular	
Pharyngobranchial	Branchiostegal rays	
Epibranchial		
Ceratobranchial		
Hypobranchial		
Basibranchial		

Vertebral Column.

Centra
Radials

Appendicular Skeleton.

Scapula	Cleithrum
Coracoid	(Clavicle)
Pelvic	Post-cleithrum
Radials	Supra-cleithrum
	Post-temporal

Dermal Skeleton.

Lepidotrichia
Scales

It will be obvious from this table that the majority if not all the cartilage-bones are ossifications in cartilage which itself is represented in the dogfish. On the other hand, there are no structures of any kind in the dogfish which have any connexion with the membrane-bones. The membrane-bones are of interest from two points of view. A number of them bear teeth : premaxilla, maxilla (not in Gadus, however), prevomer, dentary. Others enter into relations with the lateral-line canal system, and these relations are of importance, for owing to their constancy they enable homologies to be made between bones in fish and in higher Vertebrates. The lateral-line canal of the trunk runs forwards from the tail, and in so doing it pierces the scales. On reaching the head it is protected by a few " lateral-line ossicles," and then passes through the post-temporal to the pterotic and sphenotic. The supraorbital canal runs forwards over the eye through the frontal and nasal, the infraorbital canal pierces the chain of bones formed by the post-orbitals, infraorbitals, and lachrymal. The hyomandibular canal runs down through the preopercular to the dentary.

Teeth.—The teeth are fundamentally similar to the denticles or placoid scales of the dogfish, but instead of being scattered all over the surface of the body, they are restricted to the mouth. They are composed of a core of dentine containing a pulp cavity, and are covered over with a cap of enamel. The bones which bear teeth have been enumerated above.

Nervous System.—The brain and spinal cord lie in the long tubular cavity provided by the skull and neural arches of the vertebræ. The spinal cord is essentially similar to that of the dogfish, and calls for no special description. The spinal nerves, each composed of a dorsal and a ventral root, emerge between the neural arches.

In the brain, the medulla oblongata is not very different from the spinal cord. The cerebellum is well developed and projects downwards and forwards beneath the roof of the midbrain forming the valvula, a structure which is peculiar to bony fish. The roof of the midbrain is produced into optic lobes. The floor of the forebrain projects downwards as the

infundibulum, and is attached to the pituitary body and the saccus vasculosus. The latter structure, which is of doubtful significance, is peculiar to fish. It is a region of the brain-floor where the wall is thin, thrown into folds, and very richly supplied with blood-vessels. It has been supposed that its function is to secrete the cerebro-spinal fluid which fills the cavity of the brain and spinal cord, or to estimate the pressure of this fluid. The olfactory lobes are peculiar in that they are situated far forwards, close behind the nasal pits. They are connected with the rest of the brain by long olfactory tracts.

The olfactory nerves are short, which fact is correlated with the length of the olfactory tracts. The optic nerves have no chiasma. The three eye-muscle nerves, oculomotor, trochlear, and abducens, are similar to those of the dogfish, and call for no special comment. The profundus is reduced, the trigeminal has the usual maxillary and mandibular branches.
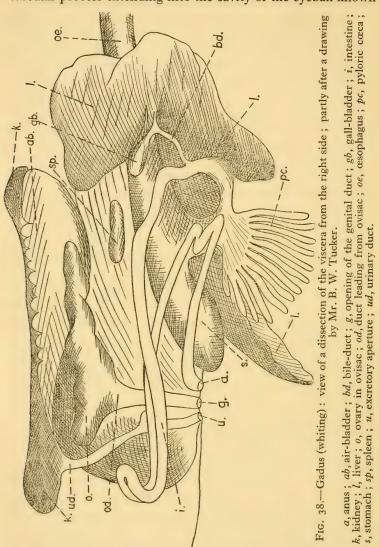
The facial nerve has ophthalmic, buccal, and hyomandibular branches, innervating respectively the supraorbital, infra-orbital, and hyomandibular lateral-line canals. In addition, the facial nerve has a cutaneous branch which runs upwards and backwards, and divides into three nerves which can be seen immediately underneath the skin. One of these runs along the base of the median dorsal fins; another runs obliquely down across the side of the body to the median ventral or anal fin; the last branch runs to the pectoral and pelvic fins.

The auditory nerve calls for no comment. The relations of the glossopharyngeal and vagus nerves to the gill-slits is the same as in the dogfish. The vagus supplies the heart and viscera, and also the lateral line of the trunk. This nerve supplying the lateral line branches, one portion remaining close to the lateral-line canal, and the other runs a little below, at the level of the septum which divides the myotomes into dorsal and ventral portions.

Sense-organs.—The nose is represented by paired nasal sacs on the upper side of the snout, each with two openings, and without connexion with the mouth. The eye is similar in structure to that of the dogfish; but there is in addition a

vascular process extending into the cavity of the eyeball known

FIG. 38.—Gadus (whiting) : view of a dissection of the viscera from the right side ; partly after a drawing by Mr. B. W. Tucker.

a, anus ; *ab*, air-bladder ; *bd*, bile-duct ; *g*, opening of the genital duct ; *gb*, gall-bladder ; *i*, intestine ; *k*, kidney ; *l*, liver ; *o*, ovary in ovisac ; *od*, duct leading from ovisac ; *oe*, oesophagus ; *pc*, pyloric cœca ; *s*, stomach ; *sp*, spleen ; *u*, excretory aperture ; *ud*, urinary duct.

as the campanula Halleri, which is attached to the retractor lentis muscle.

In the ears, the ductus endolymphaticus no longer maintains

its persistent opening to the outside. In the saccule there are two large calcareous concretions or otoliths ; otherwise the structure of the organ is similar to that of the dogfish.

The lateral-line canals have already been mentioned, and their course and innervation described.

Alimentary Canal.—The mouth leads into the pharynx, out of which the five pairs of gill-slits open. There is no open spiracle. The gill-arches between the slits are smaller than those of the dogfish, and do not form a broad septum as in that fish. This is correlated with the fact that they are covered over by the operculum. The gills are supported by two rows of branchial rays on each arch.

Behind the pharynx, the œsophagus leads to the stomach which bears a number of blind tubes, the pyloric cœca. The liver has a gall-bladder from which the bile-duct runs to the intestine. The latter receives the pancreatic duct from the pancreas, makes a loop forwards and back again and runs to the rectum, which opens at the anus.

The swim-bladder is to be regarded as a derivative of the alimentary canal, and in many forms it retains its connexion with it by an open duct. This connexion has, however, been lost in Gadus, and the swim-bladder is a closed sac which occupies the dorsal portion of the cœlomic cavity, close up against the under side of the vertebral column. Its ventral wall is thick and is covered with the cœlomic epithelium ; its dorsal wall is very thin. Inside the bladder is a rete mirabile, a concentration of small blood-vessels forming a gland which secretes oxygen into the bladder. This " red " gland, as it is called, is supplied with blood by the mesenteric artery, like the other viscera. The function of the bladder is hydrostatic, for by varying the amount of gas which it contains (by passage of gas from the blood to the bladder or vice versa) the fish can accommodate itself to any given depth of water and maintain itself there without muscular exertion. As will be seen later, it probably corresponds to the lung of the air-breathing vertebrates.

Excretory System.—A pair of mesonephric kidneys extend longitudinally, dorsal to the swim-bladder and below the

vertebral column. At their posterior ends they join, and the single median excretory duct runs ventrally, behind the swim-bladder to a urinary sinus. This opens to the exterior at the urinary aperture.

Genital System.—Gadus (and the higher bony fish) differs from the dogfish in that the urinary and genital systems are not intimately connected. The testes are elongated structures suspended in the cœlomic cavity on each side of the gut. They do not connect with the kidney, but join one another posteriorly, and send a single duct to open at the genital aperture. In the female, the ovaries correspond in position to the testes. The remarkable thing is that the ovaries are enclosed in sacs which lead by a single duct to the genital aperture. Here, therefore, the eggs are never shed free into the cœlom, to enter the open mouths of oviducts.

Vascular System.—The heart consists of sinus venosus, single auricle, single ventricle, and bulbus arteriosus. It is to be noticed that the muscular conus which was present in the dogfish has disappeared, and has only left its valves as a vestige. The ventral aorta gives off four pairs of afferent branchial arteries, one ascending each of the first four branchial arches. From these arches the blood is collected up into the efferent branchial arteries which run to the lateral dorsal aorta of their side. The lateral dorsal aortæ are joined together behind the gill-region to form the single dorsal aorta, and they also join in front of the gills, so that a ring is formed called the circulus cephalicus. Anteriorly the internal carotids run to the head ; behind, the dorsal aorta gives off the subclavian arteries to the pectoral fins, the cœliac and mesenteric arteries to the viscera, and continues backwards between the kidneys to the tail.

The venous system does not differ in essentials from that of the dogfish.

Gadus is a type of one of the most successful group of marine animals. It shows certain important advances over the condition of the dogfish, but when compared with higher forms most of its characters are seen to be specialised and secondary.

Characters of Gadus which show an advance over the conditions in Scyllium :

> Bone ;
> New marginal skeleton to the jaws ;
> New elements added to the pectoral girdle ;
> Swim-bladder.

Characters of Gadus which are secondary when compared with other forms :

> Continuity of the gonads with their ducts ;
> Loss of optic chiasma ;
> Loss of clavicle ;
> Loss of conus arteriosus ;
> Swim-bladder closed, and adapted to hydrostatic function.

LITERATURE

GOODRICH, E. S. Vertebrata Craniata : Cyclostomes and Fishes. Black, London, 1909.

PARKER, T. J. A Course of Instruction in Zootomy (Vertebrata). Macmillan, London, 1884.

CERATODUS, A CHORDATE WITH A LUNG

Externals.—Ceratodus is the Australian lung-fish, a group of great importance, whose only other living representatives are Protopterus in Africa and Lepidosiren in South America. It is not an uncommon thing for ancient and primitive groups of animals to have gone extinct everywhere except for definite, small, and isolated regions of the earth. These animals are therefore an example of discontinuous geographical distribution.

In shape, Ceratodus is typically a fish. The median fins
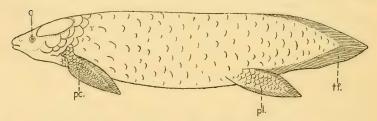
FIG. 39.—Ceratodus : view from the left side. (Partly after Goodrich.) *e*, eye ; *pc* and *pl*, pectoral and pelvic " archipterygial " fins ; *tf*, tail-fin (diphycercal ?).

are remarkable in that the dorsal, caudal, and ventral fins are all continuous with one another. Further, the tail-fin is symmetrical and pointed, and resembles the primitive diphycercal type, such as is found in Cyclostomes. There is, however, a certain amount of doubt as to whether the tail-fin of Ceratodus is primitive. When a tail such as this is derived secondarily by simplification from another type (as is the case in the eel, for example) it is called gephyrocercal.

The paired fins are elongated and leaf-like. They have a

central axis bearing radials both in front and behind, a condition known as biserial, and they conform to the type known as " archipterygial." Both the paired fins and the dorsal fin are covered with scales.

The gill-slits, five in number, are protected by an operculum. The spiracle is closed. The anterior nostrils are on the ventral surface of the snout, and behind them are the posterior nostrils which open into the mouth. There is a cloaca into which the alimentary, excretory, and genital systems open, as also do a pair of abdominal pores.

Scales.—The scales are thin and covered with spines which must not be mistaken for denticles. They overlap one another from before backwards as in Gadus, and they also extend over the dermal bones of the skull and the paired fins, and the dorsal fin.

Fin-rays.—The dermal fin-rays are jointed and made of fibrous substance. They differ from the lepidotrichia of Gadus in being more numerous than the radials, and in being covered over by scales. No actinotrichia are present, and it is uncertain whether these rays, which are called camptotrichia, represent the ceratotrichia or the lepidotrichia of Gadus.

Skull.—The skeleton is largely cartilaginous, and little of this primitive skeleton is replaced by bone. The neurocranium forms a complete case enclosing the brain, olfactory and auditory capsules, and several vertebræ are plastered on to its hind end. As some of these bear ribs, the latter appear to articulate with the skull, and are called cranial ribs. The only cartilage-bone in the neurocranium represents one of the neural arches which have been incorporated as just described. The membrane-bones which cover the dorsal surface of the neurocranium are sunk beneath the surface of the skin and are themselves overlain by scales. These bones are very modified and secondary, there is a preponderance of median unpaired bones, and as they cannot well be compared with those of other forms, there is little advantage in studying them in detail. On the underside of the neurocranium are to be found a parasphenoid, prevomer, and paired pterygo-palatines.

The splanchnocranium is important because of the manner

in which the upper jaw is fastened on to the skull. The quadrate is directly attached to the neurocranium by cartilaginous processes : a basal process and an otic process. There is also an ascending process. This method of suspension of the jaws is called autostylic ; the hyomandibula plays no part in it. The relations of the basal, otic and ascending processes to the neighbouring nerves, veins, and arteries are important, and most of them will be found to be identical in all the remaining groups of vertebrates. The ascending process lies between and separates the profundus from the maxillary branch of the trigeminal (*i.e.* it is situated between V_1 and V_2) ; the palatine nerve runs down behind and forwards beneath the basal process ; while the facial nerve (hyomandibular branch) and jugular vein pass on the inner and under side of the otic process.

The premaxilla and maxilla have disappeared, and consequently there are no teeth round the edge of the jaws. In the lower jaw the dentary is very much reduced. Teeth are carried on the prevomer, pterygo-palatine, and splenial (membrane-bone). An angular is present in the lower jaw.

In the hyoid arch there are a very small hyomandibula, and well-developed ceratohyal, hypohyal, and basihyal. The skeleton of the branchial arches also is not very well developed, and the arches do not carry any branchial rays.

The operculum is supported by opercular and subopercular bones.

Vertebral Column.—The vertebral column, which is continuous in front with the hind end of the skull, is made up of paired basidorsal and basiventral cartilaginous elements, which do not interrupt the notochord. The basidorsals rise up into bony neural arches and neural spines which are attached to the jointed radials supporting the median fin. The basiventrals in the hinder region form hæmal arches carrying hæmal spines and radials supporting the ventral median fin. Farther forwards the basiventrals are produced into ribs. These do not extend into the horizontal septum between the dorsal and ventral portions of the myotomes, like the true or " dorsal " ribs of Scyllium. Instead, they bend down and lie just

outside the outer lining of the cœlom. From their position they are known as " ventral " or pleural ribs.

Limbs and Girdles.—The primitive pectoral girdle is cartilaginous and composed of paired dorsal scapular regions, and ventral coracoid regions, which latter are joined to one another in the midventral line. Overlying this are the membrane-bones, clavicle, cleithrum, and the post-temporal which connects the girdle with the hinder part of the skull.

The pelvic girdle is formed of a median Y-shaped cartilage with the prongs directed backwards and articulating with the pelvic fins.

The fins are covered with scales. Their endoskeleton is
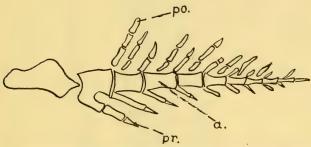
Fig. 40.—Ceratodus : skeleton of the pectoral fin, showing the " archiptery-gial " structure, with an axis (*a*), bearing preaxial (*pr*) and postaxial (*po*) radials.

cartilaginous and composed of a long central axis of about twenty pieces, tapering away to the tip. On each side of this axis are radials (pre- and postaxial). Beneath the scales are the camptotrichia.

Teeth.—The plates of teeth, which are firmly attached to the prevomer, pterygo-palatines, and splenials, are the result of fusion of separate teeth.

Alimentary Canal.—In its main lines the alimentary canal does not differ much from that of Scyllium, with a spiral valve in the intestine. Its most interesting and important feature is that in the floor of the œsophagus there is an opening (the glottis) leading to a tube or trachea which passes up round the right side of the gut to the lung. This is a large sac with

highly vascular walls surrounding a cavity which is subdivided
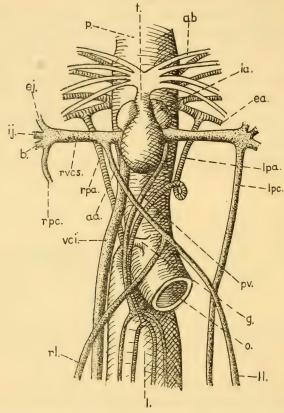
FIG. 41.—Ceratodus : diagram of the relations of the lung, heart, and vascular system seen from the ventral side (combined from diagrams after Baldwin Spencer, simplified).

aa, anterior abdominal vein ; *ab*, afferent branchial artery ; *b*, brachial vein ; *ea*, efferent branchial artery ; *ej*, external jugular vein ; *g*, glottis ; *ij*, internal jugular vein ; *l*, lung ; *la*, left auricle ; *ll*, left lateral abdominal vein ; *lpa*, left pulmonary artery ; *lpc*, left posterior cardinal vein ; *o*, œsophagus ; *p*, pharynx ; *pv*, pulmonary vein ; *rl*, right lateral abdominal vein ; *rpa*, right pulmonary artery ; *rpc*, right posterior cardinal vein (remnant) ; *rvcs*, right vena cava superior ; *t*, truncus arteriosus ; **vci**, vena cava inferior.

into little chambers or " cells." In the lung the blood can be oxygenated when the water in which the animal lives becomes

polluted, and the animal rises to the surface to take in air through the nostrils. It is this capacity of breathing by means of lungs and gills which is responsible for the name of the group Dipnoi, to which Ceratodus belongs. The lung is homologous with the swim-bladder of Gadus.

Vascular System.—Blood is supplied to the lung by branches of the last (6th) efferent branchial artery, which can now be called pulmonary arteries. The right pulmonary artery runs direct to the lung, but the left passes down under the gut and up again on the right side parallel with the windpipe or trachea. This shows that the primitive position of the lung was ventral, and that it moved up the right side, whither it is followed by the left pulmonary artery. Blood leaves the lung by the pulmonary veins, which unite to form one vein. This vein also passes down on the right side of the gut and goes right through the sinus venosus to open into the left side of the auricle. The auricle itself is partially divided into two by a septum, so that the blood (oxygenated) from the lung comes in on the left, and that from the rest of the body (deoxygenated) enters on the right from the sinus venosus. The ventricle is single, but the conus arteriosus is nearly divided into two by enlarged valves.

The ventral aorta leads forwards from the conus and gives off four pairs of afferent branchial arteries. The two collecting vessels in each gill-arch join to form the efferent branchial arteries which combine to form the dorsal aorta. The arrangement of the valves in the conus and truncus arteriosus is such that the blood from the sinus venosus tends to go into the posterior branchial arches (and so to the pulmonary arteries), while that from the pulmonary vein gets into the anterior arches. There is therefore an attempt to separate the circulation of the freshly-oxygenated blood from that of the impure blood which should go and be oxygenated.

There are two important points to notice in the venous system. The posterior cardinal on the right side loses its connexion with the ductus Cuvieri. Instead, it has developed a new connexion with the sinus venosus, forming the inferior vena cava. The ductus Cuvieri can also be called the superior

vena cava (right and left). The lateral abdominal veins unite in the midventral line and so give rise to an anterior abdominal vein, which runs into the right ductus Cuvieri close to its connexion with the sinus venosus.

The hindmost portions of the posterior cardinal veins bring blood from the posterior region of the body to the kidneys, and so form renal portal veins. Blood leaves the kidneys by the left posterior cardinal and the inferior vena cava.

Urino-genital System.—The excretory system is similar to that of Scyllium. The mesonephric kidneys are elongated, and connect by means of Wolffian ducts with the cloaca. The testis is connected with the kidney by vasa efferentia, and the Wolffian duct functions as a vas deferens. In the female, the eggs from the ovary are shed freely into the cœlom, and enter the openings of the Müllerian ducts which lead them to the cloaca.

Nervous System.—The most remarkable feature of the nervous system is the formation of cerebral hemispheres in the telencephalon (end-brain). They are hollow outgrowths from the diencephalon projecting forwards side by side. A transverse section in the region of the brain of Ceratodus therefore would show a pair of cavities, not a single cavity as in lower forms. The cavities of the cerebral hemispheres are the so-called first and second ventricles of the brain ; they communicate with the cavity of the rest of the forebrain (third ventricle) through the foramina of Monro. This is the first appearance in the vertebrate series of the organs which mean so much in the supremacy of man over other animals. In Ceratodus, the roof of the cerebral hemispheres is still membranous. The cerebellum is small.

As regards the sense-organs, the eyes and ears present no striking features. It must be remembered that the nasal sacs each have two openings. The lateral line is somewhat degenerate, and in some regions may consist of a groove instead of a canal.

Characters of Ceratodus which are lacking in other living fish, but present in Amphibia :

> Respiratory lung ;
> Pulmonary arteries and veins ;
> Divided auricle, and conus arteriosus ;
> Vena cava inferior ;
> Anterior abdominal vein ;
> Anterior and posterior nostrils : the latter within the mouth ;
> Autostylic suspension of jaws ;
> Ascending process ;
> Cerebral hemispheres.

Characters of Ceratodus which are primitive when compared with other fish :

> Cloaca ;
> Contractile conus ;
> Uninterrupted notochord ;
> Diphycercal tail ?
> Spiral valve in intestine.

Characters of Ceratodus which are secondary and specialised :

> Loss of Maxilla and Premaxilla ;
> Median membrane-bones over the skull ;
> Lack of ossification in the cartilaginous neurocranium ;
> Specialised tooth-plates ;
> Fusion of vertebræ on to the back of the skull ;
> Ventral ribs ;
> Rotation of the lung to the dorsal position.

It will be obvious from these tables that Ceratodus and the Dipnoi generally are very remarkable animals. On the one hand, they have a surprising number of characters which no other fish possess, and which are typical of Amphibia ; yet, on the other hand, their relationship with the Amphibia cannot be very close, because of the large number of specialised characters which they show.

LITERATURE

GOODRICH, E. S. Vertebrata Craniata: Cyclostomes and Fishes. Black, London, 1909.

HUXLEY, T. H. Contributions to Morphology: Ichthyopsida. On Ceratodus forsteri. Proceedings of the Zoological Society of London, 1876.

SPENCER, W. B. Ceratodus: The Blood-vessels. Macleay Memorial Volume, 1892.

CHAPTER VII

TRITON : A CHORDATE WITH 5-TOED LIMBS

Externals.—Triton, the newt, is sharply distinguished from all the types so far described, because its limbs end in fingers and toes instead of being fins. The foot has five toes, but in the newt and allied animals, the number of fingers on the hand has been reduced from five to four. Triton and all higher vertebrates are typically land-animals, and are collectively called the Tetrapoda. Some of them, however, have reverted to the condition of living in water, in varying degrees. So the whales, seals, and hosts of extinct marine reptiles have come to live almost if not entirely in water, and the newt also spends more of its time in water and is more adapted to it than its ancestors were. This secondary return to aquatic conditions is, however, easily and fundamentally distinguished from the primitive aquatic habit of the fish. The possession of typically 5-fingered, " pentadactyl," limbs is a sure criterion of a terrestrial animal, or of one whose ancestors were terrestrial. As an example of the secondary readaptation to aquatic conditions may be mentioned the webs of skin which in some species of newts extend between the fingers, and are used for swimming.

The skin is soft and slimy owing to the presence of glands, and is used largely as a respiratory surface for the oxygenation of the blood. There are no scales or fin-rays of any sort. The tail carries a continuous median dorsal and ventral fin, and in the male animals of some species, there is also a fin along the back, which becomes enlarged at the breeding season.

The first part of the life is spent in the water in which the eggs are laid and hatched, and since the early stages are aquatic

and the later ones terrestrial, these animals (newts, toads, and frogs) are called Amphibia. In the early larval condition there are external gills, and subsequently three pairs of gill-slits. These disappear when the animals metamorphose and come out on land.

The aquatic larvæ have lateral-line organs, disposed in a similar manner to those of fish, only they are sunk in a groove instead of being in a canal. When the newt emerges from the water in the summer, these organs degenerate somewhat. They reappear when the newt returns to the water, as it does at the next breeding season, if not before.

The mouth is wide, and the external nostrils are just above it. The eyes are small. The alimentary, excretory, and genital apertures are situated in a cloaca just in front of the base of the tail.
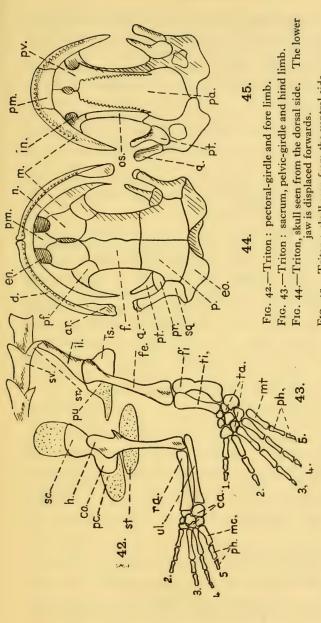
Skull.—The cartilaginous neurocranium is very similar to that of Ceratodus. The suspension of the jaws is autostylic, and besides the basal and otic processes, there is also an ascending process. These processes have precisely the same relations to the neighbouring blood-vessels and nerves as they have in Ceratodus. Only a little of this cartilaginous brain case and olfactory and auditory capsules is replaced by cartilage-bone. On each side, anteriorly, are the orbitosphenoids. Posteriorly are the prootics and exoccipitals, which form the condyles with which the skull articulates with the first vertebra.

The membrane-bones covering the skull dorsally are paired nasals, prefrontals, frontals, and parietals ; on each side of the latter are the squamosals which overlie the quadrates. On the under side are the paired prevomers, pterygoids, and the parasphenoid.

Paired maxillæ are present, and the two premaxillæ have fused together in front. The pterygoids (dermal bones) extend freely forwards from the quadrates. In the lower jaw, part of Meckel's cartilage ossifies as the articular, which is encased anteriorly between two membrane-bones ; the (lateral) dentary and the (medial) splenial. The surfaces by which the quadrate and the articular are in contact are carti-laginous. The ceratohyals and the ventral elements of the

FIG. 42.—Triton: pectoral-girdle and fore limb.

FIG. 43.—Triton: sacrum, pelvic-girdle and hind limb.

FIG. 44.—Triton, skull seen from the dorsal side. The lower jaw is displaced forwards.

FIG. 45.—Triton: skull seen from the ventral side.

ar, articular ; *ca*, carpals ; *co*, coracoid ; *d*, dentary ; *eo*, exoccipital ; *f*, frontal ; *fe*, femur ; *fi*, fibula ; *h*, humerus ; *il*, ilium ; *in*, internal nostrils ; *is*, ischium ; *m*, maxilla ; *mc*, metacarpal ; *mt*, metatarsal ; *n*, nasal ; *os*, orbitosphenoid ; *p*, parietal ; *pa*, parasphenoid ; *pc*, precoracoid ; *pf*, prefrontal ; *ph*, phalanges ; *pm*, premaxilla ; *pr*, prootic ; *pt*, pterygoid ; *pu*, pubis ; *pv*, prevomer ; *q*, quadrate ; *ra*, radius ; *sc*, scapula ; *sq*, squamosal; *sr*, sacral rib ; *st*, sternum ; *sv*, sacral vertebra ; *ta*, tarsals ; *ti*, tibia ; *ul*, ulna. The figures refer to the ordinal number of the digits.

first two branchial arches form a framework often called the
" hyoid," lying under the floor of the mouth, and of importance
in breathing. When this floor is lowered, air is drawn in
through the nostrils. These are then closed and the floor
raised, with the result that the air has to pass down the throat
and into the lungs.

Teeth are carried by the premaxilla, maxilla, prevomer,
and dentary. They are similar to the teeth of fish already
described, but now they are firmly fixed on to the bones which
carry them.

The vagus nerves emerge just in front of the back of the
skull, and the hypoglossal roots emerge behind it. Six
segments are included in the skull.

Vertebral Column.—The vertebræ are elongated cylinders,
articulating with one another by zygapophyses and cartilaginous
pads on their front and rear surfaces. The notochord is much
constricted. Each vertebra bears a pair of neural arches
above, and those of the tail also have hæmal arches beneath.
The trunk-vertebræ (except the first) bear lateral transverse
processes, with which the ribs articulate. The latter are
" true " or dorsal ribs. The first vertebra is modified in
connexion with its articulation with the condyles of the skull.
The ribs belonging to one vertebra are modified and attached
to the ilia of the pelvic girdle, forming the sacrum.

Pectoral Limb and Girdle. — The pectoral girdle is
represented only by the primitive cartilaginous girdle of the
endoskeleton, and indeed it remains largely unossified. The
dermal or membrane-bones of the girdle of other forms have
disappeared. There is a dorsal scapula, and a ventral portion
in which these may be distinguished : an anterior cartilaginous
precoracoid and a posterior partly ossified coracoid. A sternum
is present as a median plate of cartilage, overlapping the
coracoid.

The fore limb is divisible into three regions : upper arm,
forearm, and hand. The skeleton of the limbs is derived from
the radials of the fins of fish, and consequently its bones are
cartilage-bones. The bone in the upper arm is the humerus,
which fits into the glenoid cavity of the girdle, proximally.

Distally, it articulates with the radius and ulna of the forearm. The radius is the anterior of the two, *i.e.* preaxial. These two bones in turn articulate with the bones of the wrist or carpus, which is composed of seven small " carpal " bones. The radiale (scaphoid) and ulnare (cuneiform) articulate with the radius and ulna respectively. (Typically there are three bones in this proximal row, the additional one being the intermedium (lunar) which here is fused with the ulnare.) Next, there is a centrale, and the distal row of carpals is formed of four bones. The bones of the fingers are the metacarpals, and two or more phalanges, according to the finger. The first finger has been lost, so the others are numbered 2 to 5. The digital formula by which the number of phalanges is expressed, is : 0, 2, 2, 3, 2.

Pelvic Limb and Girdle.—The pelvic girdle also consists of a dorsal and two ventral elements. Dorsally, the ilium leads from the acetabulum to the modified rib of the vertebra forming the sacrum. The posterior ventral element is the ischium : both ilium and ischium are bony. The anterior element is the pubis which remains cartilaginous, and bears another cartilaginous process akin to the sternum projecting forwards. The ischium and pubis meet their fellows of the opposite side in the middle line.

Like the fore limb, the hind limb can be divided into three parts : thigh, shank, and foot. The bone of the thigh is the femur, which articulates with the acetabulum of the girdle. Distally, it joins the tibia (preaxial) and fibula of the shank. The ankle or tarsus is very similar to the wrist. The three proximal tarsal bones are separate : tibiale, intermedium (together possibly equivalent to the astragalus of higher forms), and fibulare (calcaneum). The second row is represented by the centrale (navicular), and the distal row by four bones. The proximal bones of the toes are the metatarsals, bearing the phalanges. The digital formula is 2, 2, 3, 3, 2.

Alimentary System.—The floor of the mouth carries a tongue, of which the hind edge is free.* Salivary glands are

---

* This tongue has nothing to do with the similarly named structure in Petromyzon.

present, opening into the mouth.   The glottis lies on the floor
of the pharynx and leads to the windpipe.   The stomach is
typical and the intestine makes a few loops before leading to the
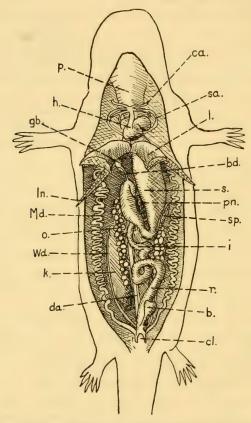
FIG. 46.—Triton : dissection of female seen from the ventral side.

b, bladder ; *bd*, bile-duct ; *ca*, carotid arch ; *cl*, cloaca ; *da*, dorsal
aorta ; *gb*, gall-bladder ; *h*, heart ; *i*, intestine ; *k*, mesonephric kidney ;
l, liver ; *ln*, lung ; *Md*, Müllerian duct ; *o*, ovary ; *p*, pharynx ; *pn*, pan-
creas ; *r*, rectum ; *s*, stomach ; *sa*, systemic arch ; *sp*, spleen ; *Wd*, Wolffian
duct.
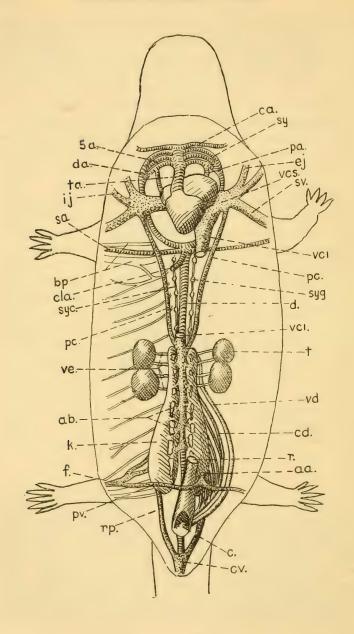
rectum, which opens into the cloaca.   Ventral to the rectum
is a sac which is formed as an outgrowth from it, the bladder.
This sac is of great importance in the evolution of the higher

vertebrates, where it gives rise to the allantois. For this reason the bladder of Amphibia is called " allantoic," to distinguish it from the swellings of the urinary ducts or " bladders " of fish. The liver is divided into several lobes, a gall-bladder is present and the bile-duct which leads from it joins the duct from the pancreas to open into the intestine.

Respiratory and Vascular Systems.—The windpipe, or trachea, leads back ventral to the gut and divides into the two bronchi leading to the lungs. These differ from the lung of Ceratodus only in that they are paired, and that they maintain their primitive position ventral and lateral to the gut. In the adult the gill-slits have disappeared, and the afferent and efferent branchial arteries are directly continuous instead of being separated by the capillaries of the gills. These arteries are now called arterial arches, and they run round the pharynx from the ventral to the dorsal side as if they were still separated from one another by the gill-slits. The ventral aorta is shortened up so much that the arterial arches come off from the truncus arteriosus, close to the heart. The 1st arterial arch runs in the mandibular arch, and the 2nd arterial arch likewise ascends the hyoid arch. Although present in the embryo, these arterial arches disappear. The 3rd arch persists as the carotid. At its base is the lingual artery which represents the anterior prolongation of the original ventral aorta. The carotid then passes through the carotid gland (see p. 401) and ascends the 3rd visceral (1st branchial) arch until it reaches a position dorsal to the pharynx. Here it turns forwards and enters the skull. It is the anterior prolongation of the original dorsal aorta.

The 4th arterial arch is known as the systemic. It goes up in what was the 4th visceral (2nd branchial) arch and turns backwards. Arrived here, dorsal to the pharynx, this vessel is exactly in the position of and corresponds to the lateral dorsal aorta of fish, only it has lost its connexion with its anterior prolongation which is now the internal carotid. This connexion, when present, is called the ductus caroticus.

The 5th arterial arch disappears in Triton, though it is present in the nearly related form Salamandra, where it leads

from the truncus up the 5th visceral arch and joins the lateral dorsal aorta.

The 6th arterial arch persists as the pulmonary. It also runs up round the pharynx and joins the lateral dorsal aorta, and, just as in Ceratodus, it gives off an artery which runs backwards to the lungs, on each side. The lungs are symmetrical, and the pulmonary arteries do not twist round the gut as in Ceratodus. The connexion between the pulmonary artery and the lateral dorsal aorta is called the ductus arteriosus, or ductus Botalli.

The lateral dorsal aortæ join one another in the middle line above the gut to form the dorsal aorta. On the way, several arteries are given off : the subclavians to the fore limbs, the cutaneous to the skin, and, near the point of junction, the cœliaco-mesenteric which runs ventrally in the mesentery suspending the gut, and supplies blood to the viscera. The dorsal aorta continues running back, supplying the kidneys on the way, and gives off the two iliac arteries which supply the hind limbs ; thence it runs on into the tail.

As in Ceratodus, the sinus venosus receives three large veins. These are the paired ductus Cuvieri or superior venæ cavæ, and the single inferior vena cava. Each superior vena cava is made up of four principal veins; external jugular (from the ventral regions of the head and tongue) ; internal jugular, corresponding to the anterior cardinal (from the dorsal regions of the head, brain, and skull) ; subclavian, itself made up of the brachial from the fore limb and the cutaneous from the skin ; and the posterior cardinal (anterior portion).

The inferior vena cava receives the hepatic veins from the

FIG. 47.—Salamandra : dissection of male seen from the ventral side.

The nerves are shown on the left and the urinogenital ducts on the right. *5a*, fifth arterial arch ; *aa*, anterior abdominal vein ; *ab*, adrenal bodies ; *bp*, brachial plexus ; *c*, cloaca ; *ca*, carotid arch ; *cd*, collecting ducts from the excretory portion of the kidney ; *cla*, cœliac artery ; *cv*, caudal vein ; *d*, dorsal aorta ; *da*, ductus arteriosus ; *ej*, external jugular vein ; *f*, femoral vein ; *ij*, internal jugular vein ; *k*, mesonephric kidney ; *pa*, pulmonary artery ; *pc*, posterior cardinal vein ; *pv*, pelvic vein ; *r*, rectum ; *rp*, renal portal vein ; *sa*, subclavian artery ; *sv*, subclavian vein ; *sy*, systemic arch ; *syc*, sympathetic nerve-chain ; *syg*, sympathetic ganglion and supra-renal body ; *t*, testis ; *ta*, truncus arteriosus ; *vci*, vena cava inferior ; *vcs*, vena cava superior ; *vd*, vas deferens ; *ve*, vasa efferentia.

liver, and the renal veins from the kidneys.   Blood returns from the tail by the caudal vein which divides into two ; each portion connects with two veins coming from the hind limb (femoral and sciatic) and runs as the renal portal vein to the kidney of its side.   All the blood from the hind regions of the body is not bound to take this course, for instead of engaging in the renal portals it may enter the pelvic veins which run towards one another, join in the midventral line, and proceed forwards as the anterior abdominal.   This vein connects with the hepatic portal vein, which collects up the blood from the intestine and takes it to the liver.

From the lungs, the pulmonary veins return the oxygenated blood to the left auricle of the heart.

The heart consists of the two auricles and the single ventricle.   It is to be noticed, however, that the septum separating the two auricles is perforated, allowing blood to pass from one side to the other.   Leading from the ventricle is the conus arteriosus, which, as in Ceratodus, is provided with valves.   The truncus represents the ventral aorta very much shortened up ; in its anterior region just before giving off the arterial arches, it is divided into two by a horizontal septum, forming a cavum pulmonale (leading to the pulmonary arch) and a cavum aorticum (leading to the systemic and carotid arches).

The circulatory system is on the whole very similar to that of Ceratodus.   It is to be noted that the separation of the venous blood from the arterial is still far from complete.   The blood is oxygenated in the lungs and in the skin.   It returns from the lungs to the left auricle by the pulmonary veins, and from the skin to the right auricle by the cutaneous, subclavian, superior vena cava, and sinus venosus.   The remainder of the blood entering the right auricle is venous.

Urino-genital System.—The mesonephric kidneys project downwards from the roof of the cœlomic cavity, covered over by cœlomic epithelium ; they are therefore more easily visible than those of fish.   The tubules of the kidneys are drained by the Wolffian ducts which lead into the bladder.   In the male, the vasa efferentia from the testis lead through the

anterior tubules of the kidney and so into the Wolffian ducts which become the vasa deferentia. The more posterior tubules of the kidney are solely excretory in function, and they do not connect with the Wolffian duct until the latter is close to the cloaca. This is a step in the direction of separating the genital from the excretory ducts, which would be effected if the ducts from the purely excretory part of the kidney were to move still farther down the Wolffian duct and eventually open directly into the cloaca.

In the female, the Wolffian ducts are solely excretory in function, and the Müllerian ducts or oviducts, which open into the cœlomic cavity anteriorly, receive the eggs and convey them down to the cloaca into which they open separately.

The kidneys retain their open ciliated funnels, leading into the cœlomic cavity (cœlomostomes).

Nervous System.—The brain has large elongated cerebral hemispheres, in the roof of which nerve-cells appear. The floor and side of the hemispheres form the corpus striatum. The cavities of these hemispheres (1st and 2nd ventricles) communicate with that of the diencephalon (3rd ventricle) by the foramina of Monro. The pineal projects upwards from the roof, and the infundibulum down from the floor of the diencephalon ; and a choroid plexus projects into the 3rd ventricle. There is no saccus vasculosus. The roof of the midbrain forms the optic lobes which are joined in the middle line, and do not present a double appearance. The hind brain has a cerebellum and a choroid plexus projecting into the 4th ventricle.

The cranial nerves are similar to those of the dogfish, except for the fact that the disappearance of the lateral-line organs (or their very great reduction) entails the disappearance of those nerves which supply them, viz. superficial ophthalmic, buccal and mandibularis externus of the facial, and lateralis of the vagus. There is a further simplification owing to the closure of the gill-slits. The glossopharyngeal is distributed to the tongue and pharynx. The vagus supplies the muscles of the larynx, and also sends parasympathetic fibres to the heart, stomach, and intestine. The hypoglossal comes out behind

the skull and is counted as the 1st spinal nerve ; it runs to the muscles beneath the tongue which actuate the " hyoid " plate for the purpose of breathing. The spinal nerves to the limbs are grouped, forming the brachial and sciatic plexus for the fore and hind limb respectively.

As in the dogfish, there are sympathetic nerve-chains on each side of the dorsal aorta. They continue forwards accompanying the internal carotids into the head. They join the sympathetic ganglia to one another, each receiving in addition a ramus communicans from its corresponding spinal nerve.

Sense-organs.—The lateral-line sense-organs have already been mentioned. The ears are in a degenerate condition in Triton, for although they appreciate vibrations in air, *i.e.* sound, their structure is not typical of land-vertebrates, and will not be considered here. It may be mentioned, however, that the tympanic cavity which is characteristic of the ears of other Tetrapods and which is homologous with the spiracular slit of the dogfish, is not developed ; and that the ear-drum or tympanic membrane is also absent.

The lens of the eye is attached to a protractor lentis muscle, contraction of which increases the distance between the lens and the retina and accommodates the eye for near vision. There is a retractor bulbi muscle which pulls the eyeball in, and depresses the roof of the mouth, which action assists in the process of swallowing.

Mesoderm and Cœlom.—An important feature is that the wall separating the pericardium from the perivisceral cœlom is very thin and membranous, and unlike the stiff partition present in the dogfish and Gadus. The amphibian condition is already foreshadowed in Ceratodus, and it results in the fact that the heart and pericardium project back into the perivisceral cavity, ventral to the gut.

The first three somites give rise to the eye-muscles. The 4th disappears during development, and the 5th produces muscle-fibres which persist.

Ductless Glands.—The thyroid arises from a downgrowth from the floor of the pharynx and afterwards divides into two,

right and left. The groups of vesicles of which it is composed are surrounded by connective tissue. Close to it are the parathyroids, on each side, and developed from the ventral region of the gill-slits which close up at metamorphosis. Their origin is therefore segmental, and it is worth noticing that parathyroids do not appear in vertebrates with persisting water-breathing gills.

The thymus glands arise from the dorsal sides of the gill-pouches, and are therefore also segmental in origin.

The adrenal bodies are in a very interesting condition. They consist of islands of tissue overlying the ventral surface of the kidneys and extending forward as isolated lumps at the side of the dorsal aorta. The bodies consist of two kinds of tissue : cortical, corresponding to the inter-renal of the dogfish, and medullary or chromaffine tissue, corresponding to the supra-renals of the dogfish, and like them derived from the sympathetic nervous system. The cortex (and inter-renal) is formed from the cœlomic epithelium. In the region of the kidney, the adrenal bodies are composed of both cortical and medullary tissue, as in the higher vertebrates. The bodies in front of the kidneys, however, may consist entirely of medullary tissue, as in the supra-renals of the dogfish. These animals therefore provide a very interesting intermediate condition.

The pituitary consists of four parts. The pars nervosa is formed from the floor of the infundibulum, the remaining three (anterior, intermedia, and tuberalis) arise from the hypophysis.

Characters of Triton which show an advance over the conditions in Fish, and which are typical of Tetrapoda :

> Limbs ending in digits (fingers and toes) ;
> Formation of arterial arches, short-circuiting the gill-capillaries ;
> Interruption of dorsal aorta from internal carotid ;
> Pelvic girdle composed of three elements : one dorsal and two ventral ;
> Presence of an allantoic bladder ;

Joining of cortical and medullary tissue to form the adrenal bodies ;

Parathyroid glands ;

Salivary glands.

Characters of Triton which are specialised when compared with higher forms :

Reduction of bone in the skull and girdles ;

Absence of membrane-bones in the pectoral girdle ;

Incompleteness of the interauricular septum ;

Degenerate condition of the ear.

Characters of Triton which are typical of Amphibia :

Heart with two auricles and single undivided ventricle ;

Skin naked, *i.e.* without horny scales ;

Aquatic larval stage.

CHAPTER VIII

Externals.—In general shape, the lizard is not very dissimilar from the newt, but it differs from it in one very important respect, which is characteristic of all the animals (Reptiles) of the group to which the lizard belongs. The body is covered with scales formed from the *epidermis*, and therefore totally different from the true scales of fish, which are always formed from the (mesodermal) dermis. To mark this distinction, the scales of reptiles are called corneoscutes. They cover the whole body including the limbs and head, and on the latter their arrangement does not correspond with that of the underlying bones. On the last phalanges of the fingers and toes, the scales form horny claws. Underlying the corneoscutes of the head there are ossifications of the dermis forming osteoscutes, which fuse with the underlying bones of the skull.

The skin is dry and devoid of glands. The eyes have upper and lower eyelids, and also a so-called " third eyelid " or nictitating membrane. Behind the eye is a circular area sunk slightly below the level of the skin, and covered over like a drum by the tympanic membrane or ear-drum. The external nostrils are on the side of the snout above the mouth. At the base of the tail is the cloaca, which in the male is provided with a pair of protrusible copulatory organs.

Skull.—The skull of the lizard, although well ossified, has several holes in it, separating the membrane-bones. The nasal aperture is bounded by the premaxilla, nasal and maxilla. The orbit is limited by the prefrontal, frontal, and postfrontal above, and the lachrymal, jugal, and postorbital beneath. Behind the orbit is an aperture called a temporal fossa, in

between the parietal, supratemporal, squamosal, postorbital, and postfrontal. In Lacerta this fossa is covered over by the osteoscutes mentioned above. This is not the case in Varanus, a form related to Lacerta, and in which the relations of the temporal fossa may be conveniently studied. There is a postorbital bar formed from the postfrontal, postorbital, and jugal, separating the orbit from the temporal fossa; and a horizontal temporal bar formed by the postorbital and squamosal, forming the lower border of the temporal fossa. (It
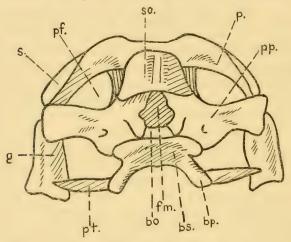
FIG. 48.—Varanus : view of the skull from behind.

bo, basioccipital ; *bp*, basipterygoid process of basisphenoid ; *bs*, basisphenoid ; *fm*, foramen magnum ; *p*, parietal ; *pf*, post-temporal fossa ; *pp*, paroccipital process (opisthotic and exoccipital) ; *pt*, pterygoid ; *q*, quadrate ; *s*, supratemporal ; *so*, supraoccipital.

should be mentioned that there remains an element of doubt concerning the homologies of the bones here called supratemporal and squamosal. See p. 440.) On the floor of the nasal capsules are the septomaxillaries, which overlie Jacobson's organs.

The quadrate abuts against the fused opisthotic and exoccipital which form the paroccipital process. The quadrate also articulates by a loose joint with the pterygoid, and is movable relatively to the squamosal and brain-case (a condition known

as streptostylic, see p. 292) ; in connexion with this arrangement the upper jaw can be raised relatively to the brain-case.

The foramen magnum is bounded by the basioccipital, supraoccipital, and exoccipital bones. In front of the basioccipital, on the floor of the skull, is the basisphenoid, which has a pair of basipterygoid processes for articulation with the pterygoids. In front of the basisphenoid is the parasphenoid.

On the palatal surface the pterygoids are long bones lying to each side of the middle line. Behind, they connect with the quadrate, their inner surfaces articulate with the basipterygoid processes of the basisphenoid, and in front each pterygoid is connected with two bones : the transpalatine laterally and the palatine medially. The transpalatine is the representative of the ectopterygoid of Gadus. In front of the palatines are the prevomers. The margin of the upper jaw is made by the premaxillæ and maxillæ. The ascending process is present and ossified as the epipterygoid, which rises as a slender pillar from the pterygoids. As in other animals, it separates the ophthalmic from the maxillary branches of the trigeminal nerve (see Figs. 138, 148, and 150).

In the lower jaw, the posterior region of Meckel's cartilage is ossified as the articular ; in addition there are the following membrane-bones : dentary, angular, supra-angular, splenial, and coronoid. Teeth are carried on premaxilla, maxilla, palatine, and dentary.

The ventral portions of the hyoid and branchial arches form a " hyoid " skeleton beneath the tongue. The hyomandibula is represented by the columella auris, a slender rod which connects the ear-drum or tympanic membrane with the fenestra ovalis in the side of the auditory capsule. This change of function of the hyomandibula from the condition in Scyllium and Gadus, where it supports the quadrate, is made possible by the autostylic method of suspension of the quadrate.

It is to be noted that the skull articulates with the vertebral column by one median condyle, and that in the formation of the skull, two more segments have been incorporated than in the Amphibia. This accounts for the fact that the hypoglossal nerves emerge from the skull, instead of behind it.

Vertebral Column.—In Reptiles and all higher vertebrates, the first two vertebræ are peculiarly modified. The first is called the atlas, and its anterior surface is hollow to receive the condyle of the skull. Its centrum has, however, been separated from it and attached to that of the second vertebra, forming the odontoid peg. Round this peg the atlas and skull are free to rotate. The second vertebra is called the axis. The subsequent vertebræ of the neck and thorax are normal, and consist of centra with neural arches and spines, and zygapophyses. The centra are concave anteriorly, and convex posteriorly, a condition described as procœlous.

The vertebræ of the tail are peculiar in that they are split transversely, and when the lizard sheds (autotomises) its tail the break occurs at one of these splits. Under some of the tail-vertebræ are Y-shaped hæmal arches, ossified as " chevron-bones."

Ribs are carried by all vertebræ in front of the sacrum except the first three ; they articulate with the centra of their respective vertebræ. The ribs belonging to the vertebræ of the neck (cervical) are short, those of the anterior region of the thorax are attached ventrally to the sternum (five pairs). The more posterior ribs (" floating ") do not touch the sternum. The two sacral vertebræ bear stout transverse processes which are attached to the ilia of the pelvic girdle.

Pectoral Girdle and Limb.—The cartilage-bones of the pectoral girdle are the scapula and coracoid, both contributing to the glenoid cavity into which the head of the humerus fits. The anterior borders of these bones are characteristically indented. The membrane-bones consist of a pair of clavicles, and a median Y-shaped interclavicle. The forelimb is typical, and similar to that of Triton except that it has five fingers, each ending in claws.

Pelvic Girdle and Limb.—The acetabulum is bordered by ilium, ischium, and pubis. The ilium points backwards towards its articulation with the sacral vertebræ. Both the ischium and the pubis meet their fellow-bones of the opposite side in the middle line, forming symphyses. On each side, the pubis and ischium are separated by the ischio-pubic foramen.

The hind limb is similar to that of Triton, but the tarsal bones undergo a modification. The proximal bones are fused into one which is attached to the tibia and fibula ; the distal bones are reduced to two, which become attached to the meta-tarsals. The result is that the ankle can only bend in one place, at the so-called mesotarsal joint. The 5th metatarsal is
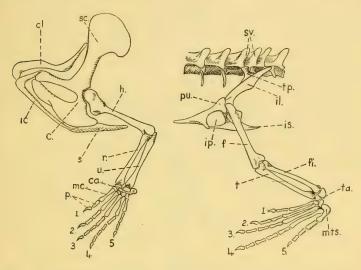
FIG. 49.—Lacerta : pectoral-girdle and forelimb, seen from the left side.

FIG. 50.—Lacerta : sacrum, pelvic-girdle and hind limb, seen from the left side.

c, coracoid ; *ca*, carpals ; *cl*, clavicle ; *f*, femur ; *fi*, fibula ; *h*, humerus ; *ic*, interclavicle ; *il*, ilium ; *ip*, ischio-pubic foramen ; *is*, ischium ; *mc*, metacarpal ; *mts*, metatarsal (note hook-like shape of that of fifth digit) ; *p*, phalanges ; *pu*, pubis ; *r*, radius ; *s*, sternum ; *sc*, scapula ; *sv*, sacral vertebræ ; *t*, tibia ; *ta*, tarsals ; *tp*, transverse processes of sacral vertebræ ; *u*, ulna.

worthy of notice on account of its peculiar hook-shaped appearance.

Alimentary System.—The tongue is long, bifid at the tip, and protrusible. It is supported by the " hyoid " skeleton. On the roof of the mouth the palatal folds appear, extending inwards from the sides. At the back of the mouth-cavity, the Eustachian tubes open. These represent the cavity of the

spiracle of the dogfish, and each is closed laterally by the ear-drum or tympanic membrane. These cavities are also called tympanic cavity, and "middle-ear," and will be referred to again in connexion with that sense-organ. The mouth is provided with salivary glands, which assist digestion.

The glottis leads to the larynx and lungs. The remaining
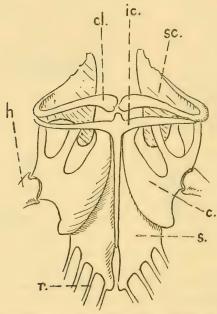
Fig. 51.—Lacerta : ventral view of the pectoral girdle and sternum.
c, coracoid ; *cl*, clavicle ; *h*, humerus ; *ic*, interclavicle ; *r*, ribs ;
s, sternum ; *sc*, scapula.

viscera do not differ sufficiently in detail from those of Triton to necessitate a specific redescription.

Respiratory System.—The lungs are sacs with very vascular walls, and they are the only respiratory organs, for the skin no longer functions as such. Another change from the amphibian condition is shown by the method of breathing. Instead of raising and lowering the floor of the mouth, the ribs are pulled forwards by muscles which run obliquely from rib to rib. At rest, the ribs slope backwards, and when pulled forwards the

effect is to increase the volume of the thoracic cavity and of the lungs. Air then rushes in.

Vascular System.—The heart consists of sinus venosus, two auricles and a single ventricle. The truncus arteriosus has been split into three right down to its base, so that the ventricle opens directly into three arteries. The more ventral of the three opens into the right side of the ventricle, and leads to the lungs, dividing as it goes into two pulmonary arteries. These no longer connect with the lateral dorsal aorta or systemic arches. The pulmonary circulation is therefore distinct. The other two vessels are the right and left systemic arches (corresponding to the systemic arches of the newt and the 4th arterial arches of fish). The right systemic arch springs from the left side of the ventricle, and the left arch from the right side of the ventricle. These vessels run up the 4th visceral arch and join dorsal to the gut to form the dorsal aorta. Now, the left side of the ventricle is occupied mostly by arterial (oxygenated) blood from the left auricle and pulmonary veins ; consequently the right systemic arch receives pure blood, more or less. But the left arch and the pulmonary vessel are on the right side of the ventricle, which contains venous blood from the right auricle, sinus venosus, and the veins of the body. In addition, there is an incomplete septum dividing the ventricle, so that while the pulmonary artery receives venous blood as would be expected, the left systemic arch receives mixed blood. The carotid arches spring from the base of the right systemic arch and therefore receive pure blood, as indeed they need, for they supply the brain. The carotid arches run dorsally in the 3rd visceral arch and when dorsal to the gut run forwards into the head as the internal carotid arteries. In addition, however, the carotid arteries connect back with the systemic arches by what are really remnants of the lateral dorsal aorta. These connexions are known as the ductus caroticus.

The arteries given off to the viscera are on the whole similar to those of Triton.

The venous system is likewise similar to that of Triton, but it is necessary to mention three new points. In correlation
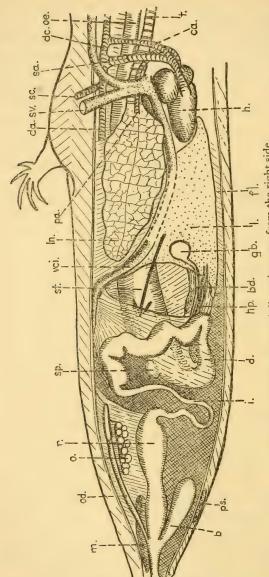
Fig. 52.—Lacerta : general dissection seen from the right side.

b, bladder (allantoic); *bd*, bile-duct; *c*, cloaca; *ca*, carotid arch; *dc*, ductus caroticus; *fl*, falciform ligament; *gb*, gall-bladder; *h*, heart; *hp*, hepatic portal vein; *i*, intestine; *l*, liver; *ln*, lung; *m*, metanephric kidney; *o*, ovary; *od*, oviduct; *oe*, oesophagus; *pa*, pulmonary artery; *ps*, pubic symphysis (cut through); *r*, rectum; *sa*, systemic arch; *sc*, subclavian artery; *sp*, spleen; *st*, stomach; *sv*, subclavian vein; *t*, trachea; *vci*, vena cava inferior. The arrow is represented as entering the omental cavity through the foramen of Winslow.

with the lack of respiratory function on the part of the skin, the cutaneous vein is not found. The posterior cardinal veins are likewise much reduced ; that on the left disappears altogether, that on the right is now known as the azygos vein. Lastly, the renal portal system is less well developed, and this is associated with the fact that the functional kidney in the adult is a new structure, the metanephros.

Urino-Genital System.—The kidneys are paired structures lying in the roof of the posterior part of the cœlomic cavity, which connect with the base of the allantoic bladder (where the latter opens into the cloaca) by means of ducts called ureters. These kidneys are not the same as the mesonephric kidneys of the animals previously described ; they are meta-nephric kidneys, and serve excretory functions only, never connecting with the genital organs. Otherwise, they are similar in structure to the mesonephros, and consist of Mal-pighian corpuscles with glomeruli and tubules. The meta-nephros develops later than the mesonephros, and out of the way of the posterior cardinal veins. The mesonephros is present in early stages of development, but does not function as an excretory organ in the adult. As the renal portal system is associated with the mesonephros, the disappearance of the one is correlated with the reduction of the other.

In the female, the mesonephros disappears in the adult, together with the Wolffian duct. The Müllerian duct persists as the oviduct and serves to convey the eggs (which drop from the ovary into the cœlom) to the exterior via the cloaca. Glands in the oviduct secrete a shell round the egg, for it is laid on dry land, and not in water. The embryo develops within a membrane, the amnion, for which reason reptiles, birds, and mammals are called Amniota. In the male, the Müllerian duct is absent, but the mesonephros and Wolffian duct persist, serving only to evacuate the sperms. The testis is connected with the mesonephros by vasa efferentia in the ordinary manner, and the tubules of the mesonephros, through which the sperms pass, form the epididymis. The epididymis is really very long, and when unravelled it forms a tube which in man is over twenty feet long. During their passage through it, the
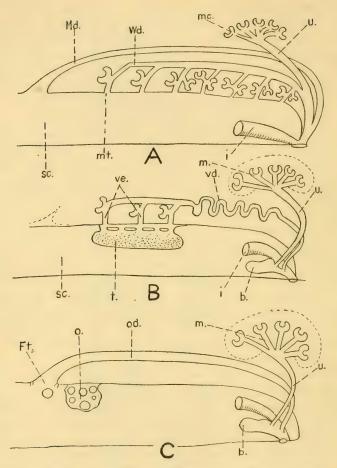
FIG. 53.—Method of formation of the kidneys in amniotes.

A, larval condition, with Müllerian duct (*Md*), Wolffian duct (*Wd*), mesonephric funnels (*mt*) opening into the splanchnocœl (*sc*); *i*, intestine. The ureter (*u*) arises from the base of the Wolffian duct and divides into a number of tubes which eventually connect with the metanephric capsules (*mc*). B, condition in the adult male. The Müllerian duct has disappeared and the Wolffian duct persists as the vas deferens (*vd*), receiving the sperms from the testis (*t*) by means of the vasa efferentia (*ve*). The ureter drains the urine from the metanephros (*m*) to the bladder (*b*). C, condition in the adult female. The Müllerian duct persists as the oviduct (*od*), the opening of which into the splanchnocœl is the Fallopian tube (*Ft*); *o*, ovary. The Wolffian duct has disappeared.

sperms are acted on by a secretion, as a result of which they complete their development and acquire the power of individual movement. The Wolffian duct is the vas deferens leading to the cloaca. As already mentioned, the wall of the cloaca bears two eversible copulatory organs, for since the egg is surrounded by a shell when it leaves the oviduct, it is obvious that fertilisation must take place in the oviduct itself.

Nervous System.—The brain is built on the same plan as that of Triton, but it shows an advance in the increased size of the cerebral hemispheres. In these there is a small amount of superficial grey matter or cortex ; in lower forms the grey matter is almost entirely within the white. This is a very important advance from the point of view of the evolution of the human brain. The sides of the telecephalon (corpus striatum) and of the diencephalon (thalamus) are enlarged, and the cavities of the 1st, 2nd, and 3rd ventricles are consequently reduced. There is a well-developed pineal eye, arising from the diencephalon, and connected with the right habenular ganglion. The cranial nerves are similar to those of Triton except for the fact that the hypoglossus (12th nerve) is included among them, and that there is a spinal accessory nerve (11th nerve). The spinal accessory supplies the dorsal muscles of the shoulder girdle, and represents a specialised portion of the vagus of lower forms.

Sense-organs.—The lateral line sense-organs are no longer present, and the sole representative of the system to which they belong is the ear. In addition to being an organ of balance, the ear is also stimulated by vibrations in air, or sound. (This is also the case in Amphibia such as the frog, but not so typically in Triton in which the ear is degenerate (see p. 100).) The vibrations impinge on the ear-drum (tympanic membrane) and are communicated to the columella auris (hyomandibula) ; the latter conveys the vibrations across the cavity of the middle-ear or tympanic cavity (spiracular visceral cleft) to the fenestra ovalis in the wall of the auditory capsule. The auditory capsule contains the auditory vesicle ; between the latter and the wall of the capsule is a fluid called perilymph, while the auditory vesicle itself contains endolymph. The

vibrations brought by the columella auris are imparted through the fenestra ovalis to the perilymph, which in turn passes them on through the wall of the auditory vesicle to the endolymph. Here the vibrations stimulate the special sensory cells. The wall of the auditory capsule has a second opening (the fenestra rotunda), situated ventrally to the fenestra ovalis. The fenestra rotunda is covered by a membrane separating the perilymph from the tympanic cavity, and its function is to damp down and deaden the vibrations in the perilymph when they reach it. With regard to the auditory vesicle itself, the utricle has the usual three semicircular canals, and the saccule, which is better developed than in lower forms in connexion with the perfecting of the sense of hearing, has a ductus cochlearis.

The retina of the eye contains mostly cones with very few rods. The lens changes its degree of convexity, and thereby its focal length, as a result of the contraction of the circular iris-muscle. The sclerotic is strengthened by bony plates. Mention has already been made of the three eyelids. The lining of the lids is in places modified into glands. At the inner side of the eye is the Harderian gland which lubricates the " third eyelid " (nictitating membrane) ; at the outer angle is the lachrymal gland. The transparent nictitating membrane, which is really a fold of the conjunctiva, is activated by a muscle derived from the retractor bulbi, and like it innervated by a branch of the abducens. The lower lid is depressed by a special muscle.

The pineal eye, already seen in Petromyzon, is remarkably developed. Its stalk rises up from the roof of the diencephalon and swells out into a vesicle of which the lower portion forms the sensory layer, and the upper forms the lens. This eye lies below the foramen between the parietals ; it is, however, covered over by connective tissue and a corneoscute.

The cavity of the nose is enlarged, and a shelf projects inwards from the side wall, increasing the surface of the nasal epithelium and forming a so-called concha. Ventral to the nasal cavities are a pair of pockets, originally formed from the nasal cavities, and lying just above the prevomers. Each opens into the mouth cavity a little way in front of the

choanæ, or internal nostrils. These structures are known as Jacobson's organ, and they probably serve to smell food in the mouth.

Cœlom.—The splanchnocoel is represented by the pericardium and perivisceral cœlomic cavities. The lungs project backwards into the latter on each side of the stomach, supported by the pulmonary folds of the cœlomic epithelium (accessory mesenteries). These folds also connect ventrally with the liver, by the pulmo-hepatic ligaments. The gut is of course suspended from the roof of the cœlomic cavity by the dorsal mesentery, and connected with the liver ventrally by the so-called lesser omentum,* also a fold of epithelium. The mesentery ventral to the liver mostly disappears, but persists anteriorly as the falciform ligament. In this manner the cœlomic cavity becomes divided up into a number of intercommunicating spaces. On each side of the gut and mesentery, and median to the pulmonary folds and pulmo-hepatic ligaments, is a pulmo-hepatic recess which ends blindly in front, and opens posteriorly into the main cavity. Owing to the kinking of the stomach to the left, the first portion of the intestine (duodenum) recurves to the right, and the right pulmo-hepatic recess forms part of a pocket, the omental cavity. This cavity communicates with the main cœlom on the right side by an opening, the upper and front borders of which are formed by the right pulmonary fold and pulmo-hepatic ligament ; the lower and hind borders are formed by the lesser omentum running from the duodenum to the liver, and by the mesentery supporting the duodenum. The opening is the foramen of Winslow, and its relations are important with regard to the inferior vena cava which runs down its upper and anterior border, and the hepatic portal vein, the hepatic artery, and the bile-duct which run along its lower border (see Fig. 125).

---

* The lesser omentum is equivalent to the gastro-hepatic ligament and the duodeno-hepatic ligament : portions of mesentery connecting the liver with the stomach and the duodenum respectively.

Characters of Lacerta, lacking in lower forms, and common to Amniota :

> Embryos develop on land within an Amnion and a shell ;
>
> Metanephros and ureter ;
>
> Spinal accessory and Hypoglossal nerves emerge from the skull ;
>
> Superficial grey matter (cortex) in the cerebral hemispheres ;
>
> Breathing effected with the help of the ribs ;
>
> Jacobson's organ ;
>
> Development of saccule, tympanic cavity (spiracular pouch), and conversion of the hyomandibula into the columella auria.   (Already present in the frog, though feebly developed in Triton) ;
>
> Atlas and Axis vertebræ differentiated ;
>
> Copulatory organs developed ;
>
> Ischio-pubic foramen present.

Characters of Lacerta which are typical of Reptiles :

> Skin covered with horny scales ;
>
> Ventricle of the heart incompletely divided (except in Crocodiles).

LITERATURE.

PARKER, T. J.   A Course of Instruction in Zootomy (Vertebrates). Macmillan, London, 1884.

CHAPTER IX

COLUMBA: A CHORDATE WITH WINGS

Externals.—The birds are principally distinguished by the possession of feathers, and the modification of the fore limbs into wings. The hind limbs continue to serve for terrestrial locomotion, but it is important to note that although the birds have evolved the habit of standing on two legs only, the body is still carried in a horizontal position. The mouth is toothless but bordered by a horny beak, the external nostrils are on each side of the upper beak, a little way behind the tip. The eyes have upper and lower lids, and also a " third eyelid," or nictitating membrane. The ear-drum is no longer flush with the surface of the skin, but sunk at the bottom of a tube, which is the external auditory meatus. The alimentary and urino-genital systems open at the cloaca. The tail is very much shortened, and on its dorsal side is the uropygial gland. This gland, which is the only one to be found in the skin of birds, produces a secretion with which the bird preens its feathers, and makes them waterproof. There are scales on the legs, and claws at the ends of the toes (in a very few cases also on the fingers), but no dermal ossifications of any kind are present.

Feathers.—The feathers are arranged on the surface of the body in definite tracts, called pterylæ. Feathers are formed by the epidermis (see p. 224), and are of different kinds in the various regions of the body. Those visible on the outer surface of the bird are called pennæ, which include the quill or flight-feathers and the contour feathers of the adult bird. Their typical structure may now be described.

A penna consists of a stalk (quill or rachis) carrying a vane.
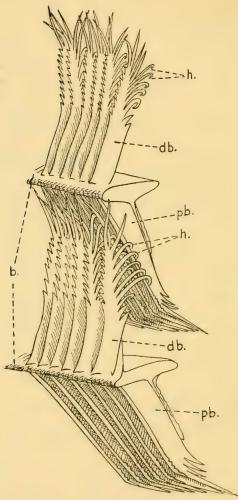
FIG. 54.—View of a portion of a feather to show the structure and relations of the barbs and barbules.

Two adjacent barbs (*b*) are represented cut off from the stalk. The barbs bear distal barbules (*db*) on the side away from the base of the feather, and proximal barbules (*pb*) on the opposite side. The hooks or hamuli (*h*) on the distal barbules of one barb are attached to the groove on the edge of the proximal barbules of the adjacent (distal) barb.

The vane is made up of a large number of barbs on each side of the central stalk or rachis, and each barb carries a number of barbules on either side. The barbules bear hooks and notches, by means of which the barbules of one barb are attached to the barbules of adjacent barbs. In this way a stiff, air-resisting plane is formed, which is especially well developed in the flight-feathers. The flight-feathers on the wings are called remiges, those on the tail rectrices. The remiges which are carried on the " forearm " (radius and ulna) are the " secondaries," those on the " hand " (carpals, metacarpals, and phalanges) are called the " primaries." Contour feathers cover the body and give it a smooth surface which presents little resistance to the air during flight. They are smaller than flight-feathers, and the hooks or hamuli on the barbules are not so well developed. Contour feathers usually possess an aftershaft, which is like a duplicate vane arising from the base of the rachis. As a rule it is small, but in the cassowary the aftershaft may be as long as the main shaft. The base of the quill beneath the vane is a hollow cylinder, opening below by the inferior umbilicus, and above at the base of the vane by the superior umbilicus. The superior umbilicus is between the main shaft and the aftershaft, which relations become obvious from a study of the development of the feather (see p. 224).

In addition to the pennæ there are in most birds down feathers or plumulæ. In these the barbules and hamuli are very degenerate so that there is no stiff vane at all. The down feathers form a dense layer which prevents the movement of the air in it, and therefore functions as a non-conductor of heat. This is important because birds are warm-blooded, and without this protection they would lose their heat rapidly by radiation from the skin to the surrounding air.

Some feathers consist only of a slender stalk with scarcely any barbs ; they resemble hairs and are known as filo-plumes.

The kinds of feathers described above are characteristic of adult birds, and may collectively be called teleoptiles. In the young birds they are preceded by nestling-feathers, or

neossoptiles. Filoplumes, plumulæ, and pennæ are preceded by prefiloplumes, preplumulæ, and prepennæ, respectively.

Feathers are usually coloured, and since they are dead structures, their colours are due either to pigment which they contain, or to the optical properties of their texture. Feathers are moulted and replaced periodically, which in many birds enables plumages of different type and colour to succeed one another. Flight-feathers are usually moulted in pairs, symmetrically right and left, as a result of which the bird is still able to fly during the moulting period.

Skull.—The skull of the pigeon, as of birds generally, is strongly ossified, so much so that the bones tend to fuse together and the sutures between them to disappear. The brain-case is much enlarged compared with lower animals. Covering the roof are : nasals, prefrontals, frontals, parietals, and squamosals (membrane-bones). The cartilage-bones of the neurocranium are : basioccipital, supraoccipital, ex-occipitals, basisphenoid, laterosphenoids, orbitosphenoids, and ethmoid. The brain-case does not extend forward between the eyes, which are only separated by an interorbital septum. The bones of the auditory capsule fuse and form the periotic.

The parasphenoid of lower forms is represented by the median rostral, and the paired basitemporals, which latter are attached to the underside of the basisphenoid. There is a single occipital condyle.

It is worth noticing that the squamosal now forms part of the wall of the brain-case ; the latter is so much enlarged that the cartilage-bones are insufficient to enclose it (see Fig. 140).

The quadrate articulates with the periotic by an otic process. Stretching forwards from the quadrates are two strings of bones on each side. On the outer side are the quadrato-jugal, jugal, maxilla, and fused premaxillæ, all membrane-bones forming the margin of the upper jaw. Median to these, the pterygoids run forwards from the quadrates, and articulate with the basipterygoid processes of the basisphenoid, and with the palatines, which run forwards to the maxillæ. Median to them are the small prevomers, fused together in the middle line.

In the lower jaw, Meckel's cartilage is represented by the articular, and the angular, supra-angular, splenial, and dentary are membrane-bones.

The hyoid skeleton is represented dorsally by the columella auris, connecting the ear-drum with the fenestra ovalis of the auditory capsule, passing behind the quadrate. Ventrally, the " hyoid " consists of basihyal, ceratohyal, basibranchial, and ceratobranchial of the 1st branchial arch.

There are no teeth in the pigeon nor in any living bird.

Vertebral Column.—The first two vertebræ are the atlas and axis. They are followed by twelve others, forming the cervical region of the vertebral column. The articulation of the centra with one another is of a peculiar saddle-like pattern called heterocœlous, and giving the neck great flexibility. The vertebræ have neural arches, zygapophyses, extra articular facets called hypapophyses, and transverse processes. The ribs articulate with the vertebræ by two heads ; a dorsal tuberculum (fitting on to the transverse process) and a ventral capitulum (touching the centrum). None of the ribs of the cervical vetebræ reach the sternum, and the first ten, carried by vertebræ 3 to 12, are actually fused with their respective vertebræ. In this manner, each of these vertebræ has a little (vertebrarterial) canal on each side. Cervical ribs of vertebræ 13 and 14 are free.

There are five thoracic vertebræ, of which the first four are fused together, and the last is fused on to the next posterior vertebra (1st lumbar). The thoracic ribs are jointed and are attached ventrally to the sternum. All the free ribs except the last bear processes (uncinate) which overlap the next posterior rib, and help to give strength to the thoracic box.

The lumbar vertebræ are six in number, and they are fused in front with the last thoracic, and behind with the two sacral vertebræ, and the first five caudals. In this way an extensive sacrum is formed, to which the ilia of the pelvic girdle are attached, strong enough to stand the leverage on the ilia due to the horizontal position of the bird's body with the legs at the hind end.

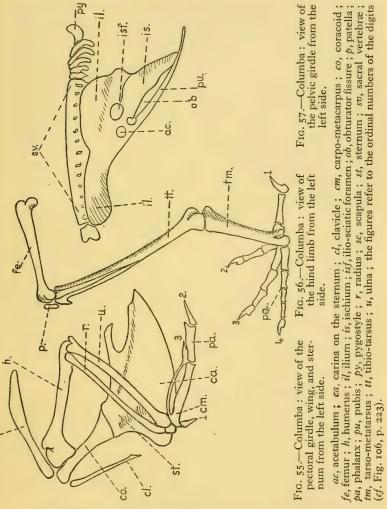After this come six free caudal vertebræ, and then four more all fused up together to make the pygostyle.

Pectoral Girdle and Limb.—The shoulder girdle is formed of scapula and coracoid (cartilage-bones), and a clavicle (membrane-bone) which meets its fellow from the other side in the middle line to form the furcula, or " merrythought." The scapula extends backwards over the ribs ; the coracoid is attached to the sternum.   Where the scapula, coracoid, and clavicle meet, they enclose a foramen (triosseum) between them, which acts as a pulley through which the tendon of the minor pectoral muscle passes, to be inserted on the humerus and so raise the wing.

The sternum is remarkable for its relatively enormous median keel or carina.   On each side of it the pectoral muscles are inserted.   Of these, the minor pectoral muscles have been mentioned above ; the major pectoral muscles pull the wing down and in so doing lift the bird in the air.   The difference between " red meat " and " white meat " can be well shown in the pectoral muscles of different birds.   Muscles which perform long-continued actions are rich in sarcoplasm and hæmoglobin, and are therefore red.   Other muscles, the action of which is not continuous, are poor in sarcoplasm, and their fibres are therefore white in colour.   The falcon is a bird which spends long periods on the wing, during which its pectoral muscles are in continuous activity.   It is not surprising to find therefore that these muscles are " red meat." On the other hand, the domestic fowl does not use its pectoral muscles continuously, and they are white.

The skeleton of the wing consists of humerus, radius, and ulna.   The wrist and hand are somewhat modified ; there are two free proximal carpal bones, the radiale and ulnare ; but the distal carpals have fused with the three fused metacarpals to form a carpo-metacarpus.   The first digit is represented by a phalanx bearing feathers which form the " bastard wing." The remaining two digits have two and one phalanges respectively, and they, together with the carpo-metacarpus, bear the primary remiges.

Pelvic Girdle and Limb.—The pelvic girdle is at first sight

different from that of any animal so far described. The
acetabulum is perforated, and is formed from the usual three
bones, ilium, ischium, and pubis. The ilium extends forwards

FIG. 57.—Columba : view of
the pelvic girdle from the
left side.

FIG. 56.—Columba : view of
the hind limb from the left
side.

FIG. 55.—Columba : view of the
pectoral girdle, wing, and ster-
num from the left side.

ac, acetabulum ; *ca*, carina on the sternum ; *cl*, clavicle ; *cm*, carpo-metacarpus ; *co*, coracoid ;
fe, femur ; *h*, humerus ; *il*, ilium ; *is*, ischium ; *isf*, ilio-sciatic foramen ; *ob*, obturator fissure ; *p*, patella ;
pa, phalanx ; *pu*, pubis ; *py*, pygostyle ; *r*, radius ; *sc*, scapula ; *st*, sternum ; *sv*, sacral vertebræ ;
tm, tarso-metatarsus ; *tt*, tibio-tarsus ; *u*, ulna ; the figures refer to the ordinal numbers of the digits
(*cf.* Fig. 106, p. 223).

and backwards and is attached to the long sacrum. The
ischium is fused along the greater part of its length with the
posterior part of the ilium, leaving an ilio-sciatic foramen

through which the sciatic artery and nerve run to the hind limb. The pubis is remarkable in that it points backwards and runs along the ventral border of the ischium, from which it is separated by the obturator fissure (corresponding to the ischio-pubic foramen, and serving for the passage of the obturator nerve). Neither the pubis nor the ischium extend to the middle line ; they consequently do not meet their fellows of the opposite side, and have no symphyses. The absence of symphyses may be correlated with the fact that birds lay relatively very large hard-shelled eggs.

The femur is short and thick ; covering the front side of its lower extremity is the patella. The tibia is fused with the fibula and with the proximal tarsal bones to form the tibio-tarsus. The distal tarsals are fused on to the united metarsals of the 2nd, 3rd, and 4th toes to form the tarso-metatarsus. The 1st metatarsal is small and free ; the digital formula of the phalanges is 2, 3, 4, 5, 0 (there being no 5th toe). The terminal phalanges bear claws. The first toe is in birds usually directed backwards, and it is opposable to the other digits. This arrangement enables a bird to stand securely on a narrow twig of a tree, with the first toe clasped round behind the twig and the remainder in front of it. The joints of the toes are bent by tendons which run back beneath the foot and up behind the tarso-metatarsus. The more the tarsal joint is bent (in squatting), the tighter these tendons are stretched, and the more strongly are the toes bent. The bird can therefore ensure a tight grip on its perch without effort, and even when asleep, simply by squatting.

It is obvious that the hind limb can bend only at the knee and between what were the proximal and distal rows of tarsals : this extreme form of the meso-tarsal joint is the rule in birds.

It is to be noted that the bones of the bird's skeleton are very light, and that most of them are hollow ; some of these spaces communicate with the air-sacs which will be described in connexion with the respiratory system.

Alimentary System.—The tongue is small and pointed, and behind it the two Eustachian tubes open into the mouth by a single common aperture. The glottis in the floor of the gullet

leads to the lungs. The gullet swells out into the crop at the base of the neck. This is a thin-walled sac in which the food is temporarily stored. The stomach is modified in that the glands are restricted to an anterior chamber, the proventriculus. Following on this is the gizzard, which has thick hard walls, and in which the food is crushed up with the help of stones and grit. The duodenum leads out from the gizzard, and receives the three ducts from the pancreas, and the two bile-ducts from the liver, which does not possess a special gall-bladder. The intestine is coiled, and leads to the rectum, which bears a pair of cœca. The rectum leads to the cloaca which is peculiar in that it is subdivided into three regions. That into which the rectum opens is called the coprodæum; next comes the urodæum, into which the ureter and genital ducts lead; and lastly the proctodæum which opens to the exterior. Into the proctodæum opens the bursa Fabricii, a blind sac-like organ of unknown significance.

Cœlom.—A knowledge of the relations of the cœlom is necessary for a proper understanding of several of the organs in birds. As in the lizard, the lungs are contained in folds of the cœlomic epithelium which connect with the liver (forming pulmo-hepatic ligaments), but in addition, these ligaments make a connexion with the side wall of the general cœlomic cavity. In so doing, they slant downwards and laterally from the roof of the cœlomic cavity, and are called the oblique septa. They separate a portion of the cœlomic cavity on their upper and outer sides, from the remainder of the perivisceral cœlomic cavity, forming the pleural cavities. Into these cavities the lungs project. The gizzard is connected with the floor of the cœlomic cavity by a post-hepatic septum, so that altogether the cavity of the cœlom is considerably obstructed and divided up. The pericardium is, of course, separated off from the rest of the cœlom by the transverse septum, but it is important to notice that in birds there is no diaphragm (see Fig. 126).

Respiratory System.—The glottis leads into a long trachea or windpipe, strengthened by cartilaginous and bony rings. This trachea divides into the two bronchi, and at the point of division a membrane extends forwards and projects into the

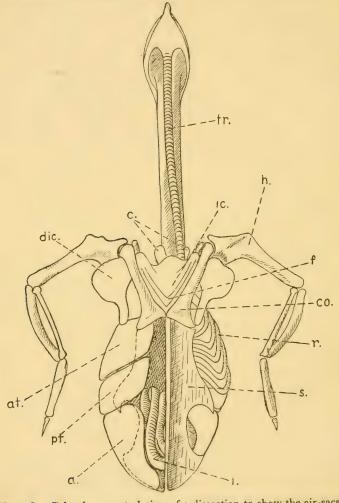trachea from the angle between the bronchi, forming the

FIG. 58.—Columba : ventral view of a dissection to show the air-sacs.

a, abdominal air-sac ; *at*, anterior thoracic air-sac ; *c*, cervical air-sacs ; *co*, coracoid ; *dic*, diverticulum of the interclavicular air-sac ; *f*, furcula ; *h*, humerus (which contains a diverticulum from *ic*) ; *i*, intestine ; *ic*, interclavicular air-sac ; *pt*, posterior thoracic air-sac ; *r*, rib ; *s*, sternum ; *tr*, trachea.

syrinx, by the vibrations of which birds sing. The bronchi

lead to the lungs which are closely pressed up against the ribs. The cavity of the lungs is repeatedly subdivided, giving them the appearance of being filled with a very vascular and spongy material. They are no longer simple hollow sacs with large undivided cavities as in the lower forms. The lungs of the bird are peculiar in that they give off a number of pouches or air-sacs, which extend into many parts of the body. There are nine of these air-sacs, arranged in the following manner : a pair of cervical sacs at the base of the neck on each side ; an interclavicular sac in the region of the furcula ; two pairs of thoracic sacs, and a pair of abdominal sacs. The bronchi lead through the lungs, into which they give off a few air-passages, to the air-sacs. The walls of the air-sacs are not vascular and no respiratory exchange takes place in them ; they act as reservoirs, and when the body cavity is compressed by raising the sternum, the air in them is forced into the lungs and out again. The efficiency of the respiratory system of the bird is due to the fact that there are no blind ends, and the air in the spaces of the lungs is completely refreshed at each expiration. It is worth noticing that the temperature of the body of birds is remarkably high (about $42°$ C.), and this is connected with the efficiency of the respiratory exchange. Expiration is the active process, by dropping the sternum the air-sacs expand and fill again. It may be remembered that several of the bones are hollow, and diverticula of the air-sacs extend into them, as for example those of the interclavicular sac into the humerus.

Vascular System.—The heart of the bird is not unlike that of the lizard, but the ventricle is completely divided into two by an interventricular septum. The pulmonary arch is present in the bird just as it is in the lizard, and it leads from the right ventricle to the lungs. The right aortic (or systemic) arch is also present, arising from the left ventricle. The left arch which in the reptile arises from the right side of the ventricle and receives mostly venous blood, has disappeared completely in the bird. All the venous blood returns to the heart from the superior and inferior venæ cavæ direct into the right auricle, there being no sinus venosus. All this blood passes into the right ventricle and to the lungs, from which the

arterial blood returns to the left auricle. The systemic arch therefore receives nothing but pure arterial blood from the left ventricle, into which it has passed from the left auricle. There are therefore two completely separate circulations in the heart, and this is rendered possible by the fact that the heart is four-chambered, both auricle and ventricle being completely divided longitudinally.

The right systemic arch gives off a pair of arteries which run forwards for a short distance, known as the innominate arteries. Each divides into two, forming the carotid arteries and the subclavians. The carotids run forwards to the head ; the subclavians supply the pectoral muscles and the wings. The systemic arch runs up on the right side of the gut and reaches a position dorsal to it where it is known as the dorsal aorta. It gives off cœliac and mesenteric arteries to the alimentary canal, and sciatic arteries to the legs, and then divides to form the iliac arteries and the caudal artery which supply the hinder regions of the body.

The superior venæ cavæ receive the jugular veins, and these are peculiar and interesting in that the right and left veins are connected by a cross-channel at the top of the neck. In the twisting of the long and flexible neck, it may happen that the vein on one side is squeezed, and the flow of blood in it interrupted. This blood can, however, return to the heart by passing across the connexion just described, and down the jugular vein of the other side. The superior venæ cavæ also each receive a subclavian vein made up of a brachial vein from the wing and a pectoral vein from the pectoral muscles.

The inferior vena cava receives the hepatic veins, and is formed by the junction of a pair of iliac veins. These receive the femoral veins from the legs and the renal veins from the kidneys. The blood in the hinder regions of the body is led forwards in a caudal vein, which soon divides into three. Two of these vessels represent the renal portal veins of the lower vertebrates, but in the adult bird these veins connect direct with the iliac veins and vena cava inferior, without breaking down into capillaries in the kidneys at all. There is therefore no renal portal circulation. The third vessel into which blood
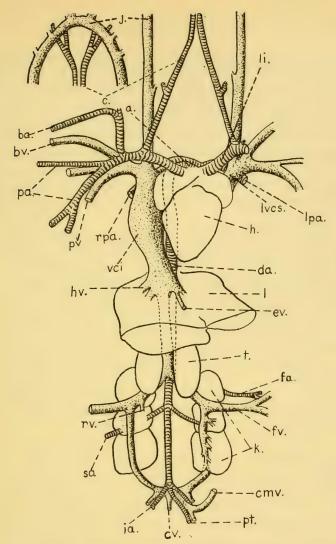
FIG. 59.—Columba : ventral view of a dissection of the vascular system ;
after a drawing by Mr. B. W. Tucker.

a, aorta ; *ba*, brachial artery ; *bv*, brachial vein ; *c*, carotid artery ; *cv*,
caudal vein ; *cmv*, cœliaco-mesenteric vein ; *da*, dorsal aorta ; *ev*, epigastric
vein ; *fa*, femoral artery ; *fv*, femoral vein ; *h*, heart ; *hv*, hepatic vein ;
ia, iliac artery ; *j*, jugular vein ; *k*, kidney ; *l*, liver ; *li*, left innominate
artery ; *lpa*, left pulmonary artery ; *lvcs*, left vena cava superior ; *pa*,
pectoral artery ; *pt*, posterior mesenteric artery ; *pv*, pectoral vein ; *rpa*,
right pulmonary artery ; *rv*, renal vein ; *sa*, sciatic artery ; *t*, testis ; *vci*,
vena cava inferior.

K

may flow from the caudal vein is the coccygeo-mesenteric vein, which runs downwards and forwards in the mesentery supporting the intestine, and joins the (hepatic) portal vein. The latter runs from the intestine and duodenum to the liver, as in all vertebrates. There is one more vessel worthy of mention, and that is the epigastric vein which runs forwards from the mesentery, passes ventral to the liver, and joins the hepatic vein. This epigastric vein represents the anterior region of the anterior abdominal vein of lower forms : the hinder part of this vein is represented in the bird by the coccygeo-mesenteric vein.

The chief difference, therefore, between the venous systems of the bird and the lizard, is the direct connexion of the " renal portal veins " with the inferior vena cava in the former. It may also be noted how the great development of the pectoral muscles has brought about a modification of the vascular system, in the form of the well-developed pectoral arteries and veins. These muscles, on which the flight of the bird depends, are the most active in the body.

Urino-genital Systems.—The kidneys are metanephric, not mesonephric. The kidneys lie in the roof of the cœlomic cavity, and each is divided into three lobes. Each kidney is connected by a ureter with the urodæal division of the cloaca. There is no bladder.

In the male, the testes are connected with the cloaca (urodæum) by the vasa deferentia, or Wolffian ducts. In the female, the right ovary and right oviduct as a rule disappear ; there is then only one ovary (the left) and one oviduct (also the left) or Müllerian duct in the adult bird. The reason for the suppression of one ovary and duct is presumably that if two eggs were to be laid simultaneously (one by each oviduct), their combined size would block the passage between the two sides of the pelvic girdle. The Wolffian ducts are not present in the female, and the male has no Müllerian ducts.

Nervous System.—In the brain, the cerebral hemispheres are well developed, and considerably larger than in the lower forms. This increase in size is due to the enlargement of the corpus striatum, and not to the development of the cortex or

superficial layer of grey matter forming the roof of the hemispheres. The cortex of the brain in birds is thin, and markedly different in this respect from that of the mammals. The cerebellum is also well developed as is the rule among animals which rely on a sense of balance, and its surface is thrown into ridges. The median portion of the cerebellum is known as the vermis, on each side of which is a conical projection known as the flocculus. The front of the cerebellum is in contact with the hinder surface of the cerebral hemispheres, and the optic lobes which form the roof of the midbrain are thrown to the side.

As in the reptiles, there are twelve pairs of cranial nerves, the spinal accessory and hypoglossal being included in the skull. The wing is supplied by the brachial plexus, composed of nerves from the hind part of the neck and the front of the thorax. The leg is supplied by a femoral nerve, and a sciatic plexus and nerve, which runs through the ilio-sciatic fissure in the pelvic girdle. The obturator nerve which pierces the obturator foramen innervates the region of the acetabulum.

Sense-organs.—With regard to the sense-organs, there is not much advance over the conditions in the reptiles. The eye is elongated from cornea to optic nerve, instead of being spherical. Projecting into the posterior chamber of the eye, which is occupied by the vitreous humour (see p. 23), is an upstanding vascular structure. This structure, known as the pecten, arises from the spot (" blind spot ") where the optic nerve and artery enter the eye ; it recalls the columella Halleri which is found with similar relations in the eye of Teleost fish. The function of the pecten is still dubious, but its vascularity suggests that it is concerned with supplying oxygen to the vitreous humour and the posterior chamber generally.

Accommodation in the eye of the bird is peculiar. The junction between the cornea and sclerotic is covered on the inside by a muscle which is striated (Crampton's muscle). Contraction of this muscle results in an increase of the convexity of the outer surface of the eye : cornea and conjunctiva, which accommodates the eye for near vision. The convexity of the lens is also increased by contraction of the circular

muscle of the iris. At the same time, the contraction of the ciliary muscle pulls the hinder part of the eye forwards, and this reduces the tension on the suspensory ligaments, which are attached to the lens.

In the ear, the cochlear part of the saccule is better developed than in reptiles, and is beginning to show the spiral winding.

With the exception of the warm-bloodedness, and the complete subdivision of the ventricle of the heart, the characters which birds show, and which are not yet developed in the reptiles, are specialisations which do not appear in the mammals. Birds represent a further development of reptiles in one direction, while the mammals evolved in another direction from another group of primitive reptiles.

Characters of Columba which show an advance on the conditions in lower forms (and which are at the same time specialisations not found in mammals) :

> Feathers ;
> Modification of the pectoral limbs into wings ;
> Loss of teeth ;
> Formation of air-sacs (foreshadowed in the Chamæleon) ;
> Formation of oblique and post-hepatic septa ;
> Loss of right ovary and oviduct ;
> Very long sacrum ; and fusion of vertebræ ;
> Extreme posterior position of pubis ;
> Loss of left systemic arch.

LITERATURE

PARKER, T. J. A Course of Instruction in Zootomy (Vertebrata). Macmillan, London, 1884.

CHAPTER X

Externals.—The most obvious characteristic of the rabbit and of other mammals is the possession of hair, which, typically, forms a complete covering to the body. Hairs are more or less cylindrical epidermal structures, seated in little pits or follicles at the base of each of which is a papilla. The epidermal cells just above the papilla multiply actively and contribute new material to the hair, which in this way grows in length (see p. 234). The central axis of the hair is called the medulla, and surrounding this is the cortex (which is often pigmented), and a cuticle. The function of hair is to prevent loss of heat from the body by radiation, for mammals are warm-blooded (homothermous). It also serves for protection, and sometimes as a sensory tactile organ, as in the case of the vibrissæ or " whiskers."

The fingers and toes end in claws, likewise epidermal structures.

The skin is thicker than in the forms previously described. In the epidermis there is a great difference between the actively-growing cells at the base (stratum Malpighi), and the flat, horny cells on the surface (stratum corneum) which are continually being lost and replaced from the stratum Malpighi.

The dermis of the skin forms the basis of leather, and it commonly contains fat forming a layer which assists the animal in maintaining its internal heat. Beneath the skin are muscles which serve to move and shake it. In the region of the trunk these muscles form the panniculus carnosus ; in the head the skin muscles are concerned with movements of the

eyebrows, lips, and external ears (platysma muscles) (see p. 278).

The skin in mammals is well supplied with glands of epidermal origin, and of which there are three kinds : sudoriparous, sebaceous, and mammary. The sudoriparous or sweat-glands, are small tubes which sink into the dermis from the surface, and end blindly after a certain number of coilings. They serve to excrete water which is obtained from the neighbouring blood-vessels, and in so doing they play an important part in the regulation of the temperature of the body. The water excreted is ordinarily converted into vapour, and thereby absorbs the latent heat required for this conversion from the body.

The sebaceous glands differ from the sweat-glands in that they branch repeatedly, and that their secretion is not an extracellular and liquid, but intracellular greasy substances which are pushed out in the loaded cells themselves. These glands are usually found opening into the hair-follicles, whence the greasy secretion spreads over the hair. Other glands of this type open to the surface along the edge of the eyelids (Meibomian glands), and into depressions at the sides of the anus (perineal glands). The secretion of the latter is responsible for the smell of the rabbit.

Mammary glands or milk glands, are also characteristic of the whole order Mammalia. They occur in both sexes, but are normally functional only in the female. They are branched tubes lying between the skin and the underlying muscles on the ventral surface of the body, and opening to the surface by nipples, of which there are in the rabbit about four pairs, corresponding to the usual number of young born in a litter.

The eyes have upper and lower eyelids and a small nictitating membrane. A noteworthy feature is the presence of external ears, or pinnæ, which assist the sense of hearing, by concentrating the waves of sound.

The anus is at the root of the tail, and is separate from the urinogenital aperture, which is situated in front of it, and takes the form of a penis in the male or a vulva in the female. At the sides of the penis in adult males are the scrotal sacs which

contain the testes. This ventral position of the testes is a new feature, peculiar to most adult mammals.

Skull.—The skull has two occipital condyles, formed from the exoccipitals. The floor is formed by basioccipital, basisphenoid, presphenoid, and vomer, the latter representing the anterior portion of the parasphenoid of lower forms. The mesethmoid is perforated by a number of pores through which branches of the olfactory nerve run to the nasal sacs; it is known as the cribriform plate. Anteriorly, the mesethmoid extends as the vertical septum nasi, which separates the cavities of the nasal capsules.

The roof of the skull is formed by the supraoccipital, parietals, frontals, and nasals. The bones of the auditory capsules are fused to form the periotics, which form the hinder part of the side of the brain-case. The remainder of the side is formed by the squamosals, alisphenoids (corresponding to the epipterygoids of reptiles), and orbitosphenoids. There is a small lachrymal bone near the front of the orbit.

The margin to the upper jaw is formed by the premaxillæ and the maxillæ. From the maxillæ the jugals extend backwards and meet a process (zygomatic) of the squamosal forming (with the jugal) the " cheek bone." The roof of the mouth is a false palate, formed by flat extensions of the maxillæ and palatine bones meeting their fellows of the opposite side ventral to the true roof of the mouth, and enclosing the nasal passage. The pterygoids are small bones behind the palatines, and at the sides of the basisphenoid. The vomer representing the parasphenoid is covered over by the false palate. Large tympanic bullæ lie beneath the periotic and contain the tympanic cavity. The nasal cavities contain a number of scroll-like turbinal bones (see Figs. 143, 149, and 150).

The wall of the skull is pierced by a number of holes or foramina through which nerves and blood-vessels pass out and enter. These foramina are commonly situated between different bones, for the nerve or blood-vessel developed first and the bones formed afterwards. At first these bones are small, but as they grow they meet one another forming sutures, and foramina are open sutures. Occasionally the bone grows
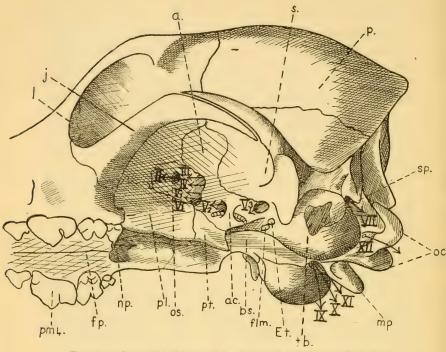
FIG. 60.—Skull of a dog, seen from the left side and slightly from beneath.

The Roman figures close to the arrows indicate the cranial nerves which emerge from the several foramina. II, optic nerve through the optic foramen ; III, oculomotor nerve ; IV, trochlear nerve ; V1, first or ophthalmic branch of the trigeminal nerve, and VI, abducens nerve, all emerging through the foramen lacerum anterius ; V2, second or maxillary branch of the trigeminal nerve, through the foramen rotundum ; V3, third or mandibular branch of the trigeminal nerve, through the foramen ovale ; VII, facial nerve, through the stylo-mastoid foramen ; IX, glossopharyngeal nerve ; X, vagus nerve ; XI, spinal accessory nerve, all emerging through the foramen lacerum posterius ; XII, hypoglossal nerve, through the condylar foramen ; *a*, alisphenoid ; *ac*, alisphenoid canal (lodging the so-called external carotid artery) ; *bs*, basisphenoid ; *Et*, opening into the tympanic bulla for the Eustachian tube ; *flm*, foramen lacerum medius through which the internal carotid artery enters the skull ; *fp*, false palate ; *j*, jugal ; *l*, lachrymal ; *mp*, mastoid process ; *np*, nasal passage ; *oc*, occipital condyles ; *os*, orbitosphenoid ; *p*, parietal ; *pl*, palatine ; *pm* 4, fourth premolar modified into the carnassial tooth ; *pt*, pterygoid ; *s*, squamosal ; *sp*, styloid process ; *tb*, tympanic bulla.

all round the nerve or blood-vessel, and the foramen then pierces that bone. The most important foramina are those in the orbit and hinder region of the skull, and they are most conveniently studied in the skull of a young dog, in which the sutures between the bones are still plainly visible.

The optic nerve (II) emerges through the optic foramen in the orbitosphenoid bone. Immediately behind this is the foramen lacerum anterius between the orbito-sphenoid and the alisphenoid. Through it pass the oculomotor (III), trochlear (IV), abducens (VI), and the ophthalmic branch of the trigeminal nerve (V1). The maxillary branch of the trigeminal (V2) emerges through the foramen rotundum in the alisphenoid, while the mandibular branch of the same nerve (V3) passes through the foramen ovale between the alisphenoid and the periotic. The Eustachian tube passes into the tympanic bulla through an opening between the latter and the basisphenoid. The foramen just median to this is the lacerum medius (likewise between the tympanic bulla and the basisphenoid), through which the internal carotid artery pierces the skull. The so-called external carotid artery which is given off from the internal carotid before the latter enters the skull, runs forwards through the alisphenoid canal. This is not a true foramen for it does not lead into the skull, but is a short tunnel in the alisphenoid. Its hind entrance is below the foramen ovale, and its anterior exit is confluent with the foramen rotundum. The facial nerve (VII) emerges through the stylo-mastoid foramen, between the hind face of the tympanic bulla and the periotic. Between the periotic and the exoccipital is a large elongated opening, the foramen lacerum posterius. Through this pass the glossopharyngeal (IX), the vagus (X), and the spinal accessory (XI) nerves, and the internal jugular vein. The hypoglossal nerve (XII) passes through the condylar foramen in the exoccipital. The large hole at the back of the skull for the spinal cord is the foramen magnum.

The lower jaw consists of a single bone : the dentary, which articulates with the skull by means of the squamosal. This method of articulation is characteristic of mammals, and

differs from the articular-quadrate articulation of all other Gnathostomes. Indeed, at first sight, the quadrate and articular appear to be absent from the mammalian skull. On the other hand, whereas other vertebrates have one single bone connecting the tympanic membrane with the fenestra ovalis of the auditory capsule, in the mammal there are three such bones. The one nearest to the fenestra ovalis is perforated and called the stapes (stirrup); it is homologous with the columella auris and hyomandibula of lower forms. The next bone is the incus, which is in reality the quadrate as can be shown by its embryological development; and the last bone is the malleus which is in reality the articular. During the course of the evolution of the mammals, these bones have therefore undergone a remarkable change of function.

The " hyoid " is a small plate of bone, connected with the periotic by a number of small bones representing the hyoid arch (styloid process). The ceratobranchials of the 1st branchial arch are represented by the posterior horns of the hyoid (thyrohyoid). Elements of the remaining branchial arches are possibly represented in the cartilages of the larynx and of the trachea.

Teeth.—Equally distinctive of mammals are the teeth, which are of different shape in the various regions of the mouth, a condition termed heterodont as distinct from the homodont condition of lower forms in which all the teeth are alike. A further distinction lies in the fact that the teeth are replaced once only in the mammal (diphyodont condition), and not repeatedly as in lower forms (polyphyodont). There are four kinds of mammalian teeth : incisors, canines, premolars, and molars. The incisors or cutting teeth are situated at the front of the mouth, those of the upper jaw are borne on the premaxillæ. The next kind of tooth is the canine or tusk, but it is not present in the rabbit, which is a herbivorous animal. In the dog the canines are well developed; that in the upper jaw is the most anterior tooth in the maxilla, and the canine of the lower jaw lies in front of that in the upper when the mouth closes. In the rabbit there is a long gap or diastema between the incisors and the premolars. Premolars and molars are

often much alike, but their distinction lies in the fact that the premolars appear in two sets : " milk teeth " arising first and being replaced by permanent teeth as in the case of incisors and canines ; but there is only one generation of molars. Premolars and molars or grinding teeth, are the hindmost teeth to be carried on the maxillæ in the upper jaw.

Bearing in mind the four different sorts of teeth, it is possible to describe the dentition of a mammal very simply and quickly by means of a " dental formula " : that of the rabbit is :

$$i\frac{2}{1}, \quad c\frac{0}{0}, \quad p\frac{3}{2}, \quad m\frac{3}{3}.$$

The dental formula of the dog, on the other hand, is :

$$i\frac{3}{3}, \quad c\frac{1}{1}, \quad p\frac{4}{4}, \quad m\frac{2}{3}.$$

Most mammalian teeth grow to a certain size and then cease, as a result of the closing of the entrance into the pulp-cavity by the formation of " roots " or fangs. Some, however, retain the open pulp-cavities which are continuously supplying food material to the odontoblasts, as a result of which the tooth can go on growing throughout life. Such teeth are called " rootless," or " with persistent pulps," and examples are to be found in the incisors of the rabbit. As a rule, teeth which are subjected to perpetual wearing down owing to grinding or gnawing, or which can grow out of the mouth for unlimited distances such as the tusks of the elephant, are of this kind. In the rabbit, the lower incisors are kept in check by the upper ones, and vice versa ; but if one tooth through accident is lost or destroyed, the opposing tooth in the other jaw is no longer resisted in its growth. Under such circumstances it grows continuously and eventually kills the rabbit by preventing it from shutting its mouth. In a sense, it may be compared with the unruly growth of a tumour.

Skeleton.—The skeleton of mammals has a peculiarity in many of its bones which is not found in any other vertebrates. Several of the cartilage-bones, and especially the vertebræ and the bones of the limbs are composed of three pieces : a central

shaft or diaphysis and an epiphysis at each end. Between the epiphyses and the diaphysis there are, in young mammals, portions of cartilage, and the bone is able to increase in length by adding on new bone to the diaphysis at each end. Eventually, however, the epiphyses become firmly fused on to the diaphysis, and no further growth of the bone is then possible.
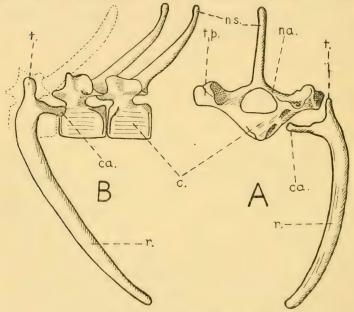

FIG. 61.—Lepus : thoracic vertebræ and ribs.

A, seen from in front ; B, seen from the left side. *c*, centrum of the vertebra ; *ca*, capitulum of the rib ; *na*, neural arch ; *ns*, neural spine ; *r*, rib ; *t*, tuberculum of the rib ; *tp*, transverse process.

The epiphyses can still, however, be recognised as distinct from the diaphysis.

Vertebral Column.—In all mammals the number of cervical vertebræ is seven (three species only form an exception to this rule). The first is the centrum-less atlas, and the second is the axis bearing the centrum of the atlas in the form of the odontoid peg. The cervical vertebræ have vertebrarterial canals formed by the fusion of the tuberculum of the rib to the

transverse process of the vertebræ, and the capitulum of the rib to the centrum. The thoracic vertebræ are usually a dozen in number, and each is related to a pair of ribs with which it articulates by tubercular and capitular facets. Behind the thoracic region are the lumbar vertebræ, usually seven in number, and characterised by their large transverse processes. Next comes the sacral region which is attached to the ilium of the pelvic girdle, and the caudal region with vertebræ which become simpler in structure as they approach the tip.

Fore Limb and Girdle.—The pectoral girdle is formed by the scapula, which bears a ridge, the acromion, and a small coracoid process representing the coracoid of lower forms. There is no separate coracoid. The clavicle is slender, and joins the acromion to the sternum. The arm is made up of the usual bones : humerus, radius, and ulna, three proximal carpals (scaphoid or radiale, lunar or intermedium, cuneiform or ulnare) ; one central carpal (centrale), and four distal carpals (trapezium, trapezoid, magnum, and unciform) make up the wrist. There are five metacarpals, and the phalanges are 2, 3, 3, 3, 3 in number on the respective fingers.

Hind Limb and Girdle.—The pelvic girdle is formed of the usual three bones : ilium, ischium, and pubis, on each side. The ilium runs forwards and upwards from the acetabulum to the sacrum, instead of backwards as in reptiles. The pubis meets its fellow from the opposite side in the middle line, forming the pubic symphysis ; and a large obturator foramen separates the pubis from the ischium of its own side.

The femur has a large head, which fits into the acetabular cavity of the pelvic girdle, and three processes or trochanters, which serve for the attachment of muscles. The tibia is large, but the fibula is small and fused on to the tibia. Covering the front side of the joint between femur and tibia is a small bone, the patella or knee-cap.

The proximal tarsal bones are two in number : the astragalus, and the calcaneum (heel-bone). There is one centrale or navicular, and three distal tarsals. The latter are, the mesocuneiform (2nd tarsal), ectocuneiform (3rd tarsal), and the cuboid (fused 4th and 5th tarsals). The rabbit is specialised

in having lost the endocuneiform (1st tarsal), otherwise its tarsus is easily comparable to that of Triton. The foot has four toes, the 1st or hallux having disappeared. There are consequently four metatarsals, and the digital formula for the number of phalanges is 0, 3, 3, 3, 3.

It is common to find small irregular bones on the under or palmar side of the joints of several of the fingers and toes, and covering certain joints of the arm and leg. These are the sesamoid bones. They arise in connexion with the insertion of tendons on to bones. Examples are the patella, and the pisiform which underlies the joint between the ulna and the cuneiform bone of the wrist. Sesamoids are important functionally, but they have not much significance in comparative anatomy, since they are not constant from group to group.

Sternum and Ribs.—The breast-bone or sternum is subdivided into six sections, called sternebræ, and a posterior piece called the xiphisternum. The most anterior of these (manubrium) is attached to the clavicles. The first seven ribs articulate ventrally with the sternum. The dorsal part of each of these ribs is bony, the ventral part cartilaginous. The next two ribs are attached ventrally not to the sternum but to the seventh rib, and the remainder end freely and are not attached to any skeleton.

Cœlom.—An important characteristic of mammals is the fact that the perivisceral cœlomic cavity is completely divided into two by a transverse partition, anteriorly convex, the diaphragm. The lungs are in front of this diaphragm, enclosed in the pleural cavities. The pericardium is also in front of the diaphragm, but its cavity is separated from that of the pleural cavities. The remaining viscera lie in the general peritoneal cavity behind the diaphragm (see Fig. 127).
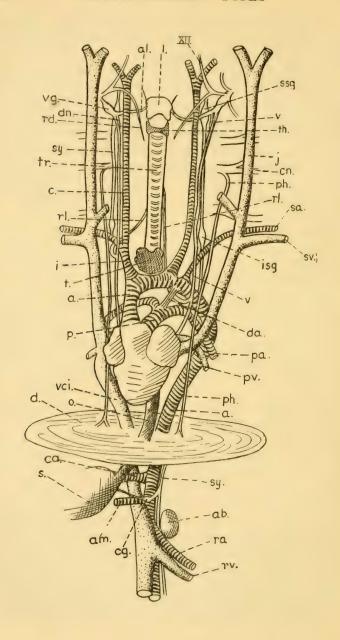
The diaphragm, which is of course pierced by the alimentary canal, the aorta, and the inferior vena cava, divides the trunk effectively into thoracic and abdominal regions. It is muscular, and plays an important part in the process of respiration, assisting the ribs in increasing the capacity of the thoracic box, and causing air to rush into the lungs. It is developed in

part from the transverse septum. The scrotal sacs contain a portion of cœlomic cavity, lined with cœlomic epithelium or peritoneum termed tunica vaginalis.

The alimentary canal is supported by a dorsal mesentery. The latter, in the region of the stomach, is called the great omentum, and is pulled ventrally and backwards so as to enclose a sac (the omental bursa) which communicates with the general peritoneal cavity on the right side of the stomach by the foramen of Winslow. In the rabbit the great omentum is small, but in other forms it is extensive and laps over the ventral side of several coils of the intestine. Fat is often found deposited in the great omentum, and especially in the pig.

The pleural cavities each surround a lung, which is suspended in them by a mesentery. The cœlomic epithelium of a pleural cavity is called the pleura, and it is divided into visceral (or splanchnic) and parietal (or somatic) parts. The parietal pleura lines the outer wall of the pleural cavity, the anterior face of the diaphragm, and in the middle line comes into contact with its fellow from the opposite side to form the mediastinal septum. The visceral pleura continues from the parietal and covers over the lung. When the ribs are lifted, the pleural cavities increase their volume, and since the space between the visceral and parietal pleura is a closed one, expansion of the parietal pleura is necessarily accompanied by expansion of the visceral pleura and of the lung which it covers. If the thoracic box were punctured and air could get into the pleural cavities, the visceral pleura and the lungs would fail to expand. The pericardium lies ventral and median to the pleural cavities.

Alimentary System.—The original edge to the mouth is represented by the gums, in which the teeth are set. Outside these, fleshy lips are developed. The roof of the mouth is formed by the false palate, due to the extension inwards of a shelf from the maxilla and palatine bone on each side. In this region it is called the hard palate, and it is continued posteriorly a short distance by the soft palate, in which there is no bone. The false palate encloses the nasal passage between itself and

the true roof of the mouth, and this passage opens into the mouth behind the soft palate, by the secondary choana. The floor of the mouth is occupied by a large soft tongue. Four pairs of salivary glands secrete into the mouth. They are, the parotid (just in front of the ear), the submaxillary (behind the angle of the mouth), the infra-orbital (below and behind the cheek-bone, and the sublingual (on the inner side of the lower jaw).

The Eustachian tubes open into the mouth near the opening of the nasal passage, and behind them are the tonsils which are remnants of the 2nd pair of visceral (1st branchial) gill pouches.

The pharynx connects with the larynx by the glottis, and this opening is protected by a flap, the epiglottis. In breathing, the soft palate is dropped, thus allowing air to come in through the nasal passage and into the mouth, and the epiglottis is raised, allowing the air to enter the larynx on its way to the lungs. When swallowing is taking place, the soft palate is raised, closing the nasal passage, and the epiglottis is forced down and bars the way into the larynx.

The œsophagus runs through the diaphragm to the cardiac portion of the stomach. The other or pyloric portion of the stomach opens into the duodenum, the opening being surrounded by a sphincter muscle. The duodenum receives the bile-duct and the pancreatic duct. The liver is large, and fits close up against the posterior face of the diaphragm. It is

---

Fig. 62.—Lepus : dissection of the vascular system seen from the ventral side.

a, aorta ; *ab*, adrenal body ; *al*, anterior laryngeal nerve (branch of vagus) ; *am*, anterior mesenteric artery ; *c*, carotid artery ; *ca*, cœliac artery ; *cg*, anterior mesenteric sympathetic ganglion ; *cn*, cervical nerve ; *d*, diaphragm ; *da*, ductus arteriosus ; *dn*, depressor nerve (branch of vagus) ; *i*, innominate artery ; *isg*, posterior cervical sympathetic ganglion ; *j*, jugular vein ; *l*, larynx ; *o*, œsophagus ; *p*, pulmonary trunk ; *pa*, pulmonary artery ; *ph*, phrenic nerve ; *pv*, pulmonary vein ; *ra*, renal artery ; *rd*, ramus descendens (branch of hypoglossal nerve) ; *rl*, recurrent laryngeal nerve (branch of vagus) ; *rv*, renal vein ; *s*, stomach ; *sa*, subclavian artery ; *ssg*, anterior cervical sympathetic ganglion ; *sv*, subclavian vein ; *sy*, sympathetic nerve-chain ; *t*, thymus gland ; *th*, thyroid gland ; *tr*, trachea ; *v*, vagus nerve ; *vci*, vena cava inferior ; *vg*, vagus ganglion ; XII, hypoglossal nerve.

connected with the stomach by the lesser omentum (mesentery), and with the floor of the peritoneal cavity by a small ventral mesentery, the falciform ligament. The gall-bladder is green in colour. The pancreas lies in the mesentery which stretches between the two arms of a loop formed by the duodenum.

The small intestine is lined with countless finger-shaped processes called villi which absorb the products of digestion. Along the wall of the intestine are masses of lymphatic tissue known as Peyer's patches, from which lymphocytes pass into the cavity of the intestine. In the rabbit the small intestine is over two yards long, and it ends in a chamber called the sacculus rotundus, with which the cœcum and the large intestine connect. The cœcum or blind gut ends blindly as its name implies, and at its extremity is the vermiform appendix which contains much lymphatic tissue. The cœcum is a structure commonly found in herbivorous animals, for in it cellulose is digested with the help of bacteria. It is usual to find it reduced or absent in carnivorous forms. The large intestine or colon connects with the cæcum near the opening of the sacculus rotundus, and leads to the rectum and anus.

Respiratory System.—Most of the structures concerned with respiration have already been described in connexion with the mouth and the pleural cavities. The larynx is protected by a number of cartilages (thyroid, cricoid, and arytenoid) to which muscles are attached. Internally, it contains the vocal cords. The trachea which is kept open by cartilaginous rings, leads from the larynx to the point where the two bronchi arise. Each bronchus leads to a lung, and becomes subdivided into larger and larger numbers of increasingly smaller air-spaces. The mammalian lung is not a vascular hollow sac such as the lung of the newt or the lizard ; its cavity is repeatedly subdivided so that it appears to be filled with spongy tissue in which blood-capillaries circulate, surrounded on all sides by the minute air-spaces. The surface of contact between air-spaces and blood-vessels is very great ; in man, for example, it is about thirty times the area of the body-surface.

Vascular System.—The heart contains four chambers, two

auricles and two ventricles. The truncus arteriosus has been split into two, right down to its base. One of these vessels opens out of the right ventricle and leads to the lungs; it is the pulmonary artery. The other opens out of the left ventricle and is the aorta which leads to the carotid arteries and the systemic arch. The two superior venæ cavæ and the inferior vena cava open directly into the right auricle; there is no sinus venosus. The pulmonary veins open into the left auricle. Guarding the opening between the right auricle and right ventricle is the tricuspid valve; the corresponding opening between the left auricle and left ventricle is guarded by the mitral valve.* The openings of the aorta and pulmonary artery are guarded by semi-lunar valves.

The systemic (4th arterial) arch persists only on the left side. On the right, it is represented only by the short innominate artery from which the right carotid and right subclavian arteries arise. On the left side these two arteries arise from the systemic arch, which, passing back and up round the left side of the gut, becomes the dorsal aorta. The dorsal aorta gives off the following arteries: cœliac (to stomach, liver, duodenum, and spleen); anterior mesenteric (to small intestine and colon); posterior mesenteric (to rectum); all of which run ventrally in the mesentery to the several viscera. Between the anterior and the posterior mesenteric arteries, the dorsal aorta also gives off the renal arteries to the kidneys, and the genital arteries to the gonads. In the case of males in which the testes have descended into the scrotal sacs, the latter arteries are of considerable length. Posteriorly the dorsal aorta divides into the iliac arteries which supply the hind legs, and the caudal artery. The 5th arterial arch disappears, but the 6th is represented by the pulmonary. Originally, as in the fish, the 6th arterial arch communicated with the lateral dorsal aorta, and this communication is present in the mammalian embryo, on the left side, in the form of the ductus arteriosus. In the adult the ductus arteriosus loses its function (which is important in the embryo) and degenerates

---

* The number of flaps which these valves possess should be obvious: the tricuspid has three, and the mitral two.

into a ligament. The ductus arteriosus is also called the ductus Botalli.

The vena cava superior of each side is made up of the jugular and subclavian veins, and opens into the right auricle. In some forms the left superior vena cava is connected with the right by a transverse innominate vein, and so loses its own opening into the right auricle. The left vena cava superior also receives at its base the thoracic duct which connects with
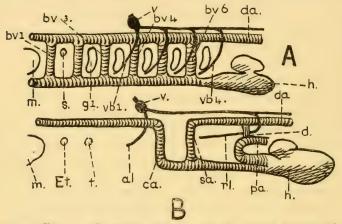

FIG. 63.—Diagram showing the relations of the arterial arches and the branches of the vagus nerve in : A, Scyllium, and B, Lepus ; seen from the left side.

al, anterior laryngeal nerve ; *bv* 1, 3, 4, and 6, blood-vessels (arterial arches) running in the first, third, fourth, and sixth visceral arch ; *ca*, carotid arch ; *d*, ductus arteriosus ; *da*, dorsal aorta ; *Et*, Eustachian tube ; *g* 1, first gill-slit ; *h*, heart ; *m*, mouth ; *pa*, pulmonary artery ; *rl*, recurrent laryngeal nerve ; *s*, spiracle ; *sa*, systemic arch ; *t*, tonsil ; *v*, vagus nerve ; *vb* 1, 4, first, fourth branch of the vagus nerve.

the system of lymphatic vessels. The posterior cardinal veins are represented by the azygos (right) and hemiazygos (left) veins of the wall of the thorax. The hemiazygos connects with the azygos, which opens into the right superior vena cava. The connexion between the hemiazygos and the left superior vena cava has been lost.

The walls of the heart itself are drained by veins, called coronary veins, which open into the right auricle.

The veins from the hind legs (iliac and femoral veins) run into the inferior vena cava, which also receives the genital vein from the gonads, the renal veins from the kidneys and the hepatic veins from the liver, and runs into the right auricle. Blood from the stomach and intestine is carried to the liver by the hepatic portal vein : there is no renal portal vein. The blood of the mammals differs from that of all other animals in that in the adult, the red blood-corpuscles have no nuclei. Instead of being biconvex, the red corpuscles here are biconcave. The source of supply of new blood-corpuscles in late embryonic and in adult life is in the red marrow which is situated in the central cavity of a number of bones. In addition, lymphocytes are produced in the lymph-glands, which also serve as blood-filters. It is possible that blood-corpuscles may also be formed in the spleen.

Like birds, mammals are warm-blooded, or homothermous.

Urino-genital System.—The kidneys are asymmetrically placed. They are metanephric structures, connected by the ureters with the urinary bladder.

In the female the Müllerian ducts persist while the Wolffian ducts disappear together with the mesonephros (traces of the latter may persist as the epoöphoron and paroöphoron). The ovaries are close to the anterior end of the Müllerian ducts or oviducts, which open into the peritoneal cavity by the Fallopian tubes. The base of each oviduct is enlarged and specialised to form the uterus, in which the young embryos develop, for mammals are viviparous. The two uteri are close together, and they open into the single median vagina. The bladder is just ventral to the vagina and connects with it to form the vestibule which communicates with the exterior by the vulva.

The vestibule is dorsal to the pubic symphysis, and ventral to the anus, with which it has no connexion. There is therefore no cloaca.

In the male, the Müllerian ducts disappear except for the uterus masculinus, which lies dorsal to the bladder. The testes are connected with the epididymis, representing the mesonephros of their own side. From the epididymis the vas deferens or Wolffian duct leads to the base of the bladder on its

dorsal side, close to the prostate gland. The bladder and vasa deferentia lead into a tube, the urethra, which runs through and opens to the exterior at the end of the penis.
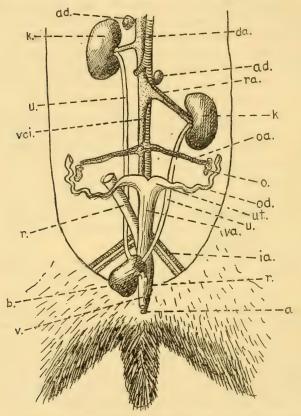
FIG. 64.—Lepus : dissection of the female urinogenital system seen from the ventral side.

For explanation of lettering, see Fig. 65.

The testes arise near the roof of the peritoneal cavity, suspended by mesenteries. When here, they are said to be in the abdominal position, for later on they descend ventrally and backwards into the scrotal sacs. The spermatic cords, containing the artery from the dorsal aorta, show the path

taken by the testes in their descent; they passed median and
ventral to the ureters as is shown also by the course of the
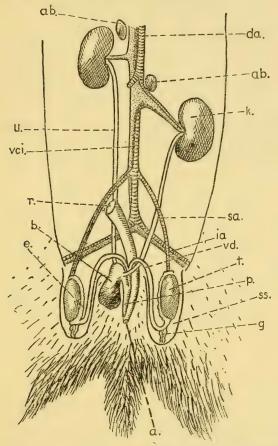
FIG. 65.—Lepus : dissection of the male urinogenital system seen from the
ventral side.

a, anus ; *ab*, *ad*, adrenal body ; *b*, bladder ; *da*, dorsal aorta ; *e*, epi-
didymis ; *g*, gubernaculum ; *ia*, iliac artery ; *k*, kidney ; *o*, ovary ; *oa*,
ovarian artery ; *od*, oviduct ; *p*, penis ; *r*, rectum ; *ra*, renal artery ; *sa*,
spermatic cord ; *ss*, scrotal sac ; *t*, testis ; *u*, ureter ; *ut*, uterus ; *v*, vesti-
bule ; *va*, vagina ; *vci*, vena cava inferior ; *vd*, vas deferens.

vas deferens. The epididymis is connected with the scrotal
sac by an elastic cord, the gubernaculum, which in early stages

grows down into the scrotal sac and guides the testis thither in its descent.

It may be mentioned that the ovary in mammals is peculiar in possessing Graafian follicles (see p. 227).

Ductless Glands (see Chapter XXXIII).—The spleen is situated in the mesentery near the stomach. It is related to the lymphatic glands, and its function is to act as a filter or purifier of the blood. This it does by destroying worn-out blood-corpuscles, and foreign bodies which may have got into the blood.

The thyroid is two-lobed, and lies across the ventral side of the larynx. It is associated with the parathyroids.

The thymus lies close in front of the heart, and is smaller in older than in younger animals. The adrenals are small compact bodies lying anterior to the kidney on each side. Each consists of a cortex (corresponding to the inter-renal of Scyllium) and a central medulla (supra-renal). The pituitary lies in a depression in the floor of the skull, called the sella turcica. The gland is composed of four parts: anterior, intermedia, tuberalis, and nervosa. The pineal gland is on the roof of the between-brain and between the cerebral hemispheres. The pancreas has already been noticed on account of its external secretion into the duodenum, but it also has a very important internal secretion formed by the islets of Langerhans. The gonads produce an internal secretion which is responsible for the differentiation of the sexual characters of their particular sex, but it is not yet clear which tissue is responsible for this effect. In the pregnant female, the follicle from which the egg was liberated becomes a corpus luteum, the internal secretion of which plays an important part in the development of the embryo in the uterus.

Nervous System.—The most important characteristics of the mammalian nervous system are to be found in the brain.

The medulla oblongata or myelencephalon is not very different from that of lower forms, but in the metencephalon the cerebellum is much enlarged and divisible into a number of lobes. Its surface is thrown into a number of folds, which increases the quantity of superficial grey matter or cortex

which it contains. There is also a band of nerve-fibres which join the two sides of the cerebellum to one another passing ventral to the rest of the hindbrain; this is the pons Varolii,
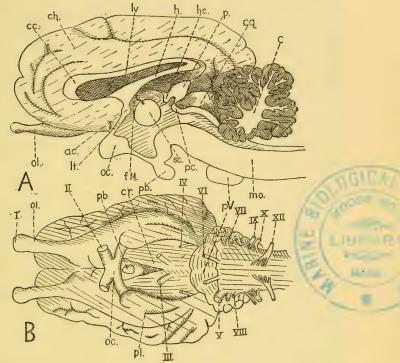
FIG. 66.—Lepus : the brain, seen, A, from the inner side of a longitudinal vertical section ; B, from the ventral side.

ac, anterior commissure ; *c*, cerebellum ; *cc*, corpus callosum ; *ch*, cerebral hemisphere ; *cq*, corpora quadrigemina ; *cr*, crura cerebri ; *fM*, foramen of Monro (shown by an arrow) ; *h*, hippocampal commissure ; *hc*, habenular commissure ; *lt*, lamina terminalis ; *lv*, lateral ventricle (cavity of cerebral hemisphere) ; *mo*, medulla oblongata ; *oc*, optic chiasma ; *ol*, olfactory lobe ; *p*, pineal body ; *pb*, pituitary body ; *pc*, posterior commissure ; *pl*, pyriform lobe ; *pV*, pons Varolii ; *sc*, soft commissure. The roman figures indicate the roots of I, olfactory ; II, optic ; III, oculomotor ; IV, trochlear ; V, trigeminal ; VI, abducens ; VII, facial ; VIII, auditory ; IX, glossopharyngeal ; X, vagus, and XII, hypoglossal nerves.

peculiar to mammals. The cavity of the 4th ventricle does not extend into the cerebellum, which is solid. The roof of the midbrain bears, not two, but four prominences. That is to

say, that in place of the two optic lobes of lower vertebrates, there are now four corpora quadrigemina.

The sides of the between-brain are thickened to form the optic thalami, so much so indeed that the two sides touch one another across the constricted 3rd ventricle, forming the " soft commissure." The roof of the between-brain bears the pineal stalk, the floor is depressed to form the infundibulum to which the pituitary body is attached. Posterior to the pituitary, the corpora mammillaria form two prominences depending from the floor. The main bundles of fibres which pass up and down from the brain and spinal cord run in the ventral portion of the hindbrain, dorsal to the pons Varolii, and diverge right and left in the region of the infundibulum forming the crura cerebri.

The cerebral hemispheres, or roofs of the lateral ventricles forming the end-brain, are enormous and extend backwards covering over the between-brain and midbrain. The superficial layer of nerve-cells or grey matter forming the cerebral cortex, which was slightly developed in reptiles, is in the mammals thick and well formed. The surface is thrown into a few folds, forming sulci and gyri ; but these are not so numerous in the brain of the rabbit as in higher mammals. The body of the hemispheres is marked out into a number of lobes by fissures (frontal, parietal, occipital, and temporal lobes). The two hemispheres are separated by a deep cleft or median fissure, but the cortex of each side is connected with that of the opposite side by a broad band of transverse fibres forming the corpus callosum, likewise peculiar to mammals. The cavities of the hemispheres are the lateral ventricles, which communicate with the 3rd ventricle by the foramina of Monro.

Beneath the temporal lobes are the pyriform lobes which correspond to part of the roof of the end-brain of reptiles, and which communicate with the olfactory lobes in front. The floor of the end-brain is marked by the optic chiasma and the corpus striatum.

The various regions and centres of the brain in mammals are extensively connected with one another by tracts of fibres. Most of these connexions can only be made out by detailed

study, but the transverse tracts or commissures are easily seen in a longitudinal section of the brain. Of these, the corpus callosum (connecting cerebral cortex) and the pons Varolii (connecting cerebellar cortex) have already been mentioned. In addition there are the following : the hippocampal commissure, which connects the two hippocampal lobes, running ventral and posterior to the corpus callosum and dorsal to the 3rd ventricle ; the anterior commissure, connecting the two halves of the corpus striatum, and running in the anterior wall of the 3rd ventricle or lamina terminalis ; the habenular commissure, connecting the optic thalami, running across the roof of the 3rd ventricle just beneath the pineal body ; the posterior commissure, in the roof of the midbrain ; the inferior commissure, crossing the floor of the 3rd ventricle close to the optic chiasma. The " soft commissure " is not really a commissure, since it does not transmit a transverse tract of fibres.

Meningeal Membranes.—The brain is surrounded by the vascular pia mater, which projects into the lateral ventricles, the 3rd and the 4th ventricles, forming in each a choroid plexus. Outside the pia mater is the arachnoid membrane, and outside this again is the protective and hard dura mater. The cerebrospinal fluid which fills the canal of the spinal cord and the ventricles of the brain communicates with the space contained by these meningeal membranes through an opening in the roof of the 4th ventricle, the foramen of Magendie.

Nerves.—The distribution of the peripheral nerves in the head is not dissimilar from that in lower forms, but attention may be paid to the conditions in the region of the neck. On each side of the neck, just lateral to the trachea, there are a number of nerves running parallel with the carotid artery and jugular vein. The vagus is one of these : it emerges from the skull (through the foramen lacerum posterius) and swells into a ganglion from which a nerve runs backwards. It soon gives off an anterior laryngeal nerve which runs to the larynx, and a small depressor nerve which accompanies the vagus in its course backwards to the heart. The vagus passes ventral to the aortic arch on the left, and ventral to the innominate artery (which corresponds to the aortic arch) on the right. Immediately after

passing the artery, the vagus gives off a posterior or recurrent laryngeal nerve which loops round the artery, passes dorsal to it, and runs forwards again along the side of the trachea. On the left side the loop of the recurrent laryngeal passes behind the ductus arteriosus. This peculiar course of the recurrent laryngeal nerve is easily understood on referring to the nervous system of Scyllium. The anterior laryngeal nerve corresponds to part of the first branch of the vagus which runs in the 4th visceral (2nd branchial) arch. The posterior or recurrent laryngeal nerve corresponds to part of the 4th branch of the vagus which runs in the 7th visceral (5th branchial) arch. Now the aortic arch, and its representative on the right the innominate artery, are the blood-vessels of the 4th visceral (2nd branchial) arch ; and the ductus arteriosus is the vessel of the 6th visceral (4th branchial) arch. In development these arches are displaced backwards to a considerable extent. But this backward movement of these arteries necessarily pulls back the nerves of the next posterior visceral arch, and this is why the recurrent laryngeal nerves have to loop round the arteries before they can reach their destination. The main branch of the vagus continues backwards to the heart, stomach, and intestine and corresponds to the visceral branch of the vagus of Scyllium. It transmits fibres which belong to the parasympathetic (autonomic) nervous system.

Parallel with the vagus in the neck is the trunk of the sympathetic nervous system. It swells into the anterior cervical ganglion, on a level with the ganglion of the vagus, and continues forwards into the head accompanying the internal carotid artery. Farther back, the sympathetic trunks have a posterior cervical ganglion, and run backwards accompanying the aorta, swelling into ganglia in most of the segments of the thorax and abdomen. From some of these ganglia, fibres run to the anterior mesenteric ganglion on the root of the anterior mesenteric artery, and to the posterior mesenteric ganglion, which is situated near the root of the posterior mesenteric artery. From these ganglia, fibres are distributed to the smooth muscles of the gut, bladder, and other viscera. It may be repeated that the feature which distinguishes the

autonomic (sympathetic and parasympathetic) nerves from the remainder, is the fact that in the autonomic system the muscles and glands are *not* connected directly with the brain or spinal cord by a *single* nerve-cell, but by two, one reaching from the brain or cord to the sympathetic (or parasympathetic) ganglion, and the other continuing from this ganglion to the muscle or gland in question. Such muscles are always smooth and
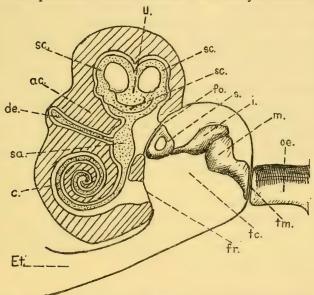
FIG. 67.—Diagram showing the structure of the ear in mammals.

ac, auditory capsule ; *c*, cochlea ; *de*, ductus endolymphaticus ; *Et*, Eustachian tube ; *fo*, fenestra ovalis ; *fr*, fenestra, rotunda ; *i*, incus (quadrate) ; *m*, malleus (articular) ; *oe*, external auditory meatus (outer ear) ; *s*, stapes (columella auris, hyomandibula) ; *sa*, saccule ; *sc*, semicircular canal ; *tc*, tympanic cavity (middle ear) ; *tm*, tympanic membrane (eardrum) ; *u*, utricle.

involuntary. Striped (voluntary) muscles are innervated direct from the brain or cord by nerve-cells which go all the way without interruption.

As in lower forms, the ganglia of the sympathetic trunk are connected with the spinal ganglia by rami communicantes.

The diaphragm contains muscles of somatic origin which are innervated by the phrenic nerves. These nerves are

formed from the 4th and 5th cervical spinal nerves, and run back to the diaphragm on each side of the heart. The length of their course shows the amount which the diaphragm, together with the heart and aortic arches, have moved backwards during development; a movement which has already been noticed in connexion with the recurrent laryngeal nerves.

Sense-organs.—The sense-organs of the mammal show certain peculiarities. The sensory surface of the olfactory organs is increased by the formation of folds supported by the turbinal bones. Jacobson's organ opens into the mouth in some forms, but it disappears in others. The ear is remarkable for the external pinna, and the inclusion of the articular and quadrate as the malleus and incus, in the chain of bones which together with the stapes (columella auris) connect the tympanic membrane with the fenestra ovalis. The projection from the saccule which forms the ductus cochlearis in lower forms, and is responsible for hearing as apart from appreciating balance (the function of the rest of the ear), is in the mammals very highly developed. It is much elongated, and is coiled in a spiral which enables it to be accommodated in the comparatively small cochlear part of the auditory capsule.

The eyelids are movable and muscular, and well supplied with glands; lachrymal and Harderian glands are present, and a naso-lachrymal duct.

Characteristics of Lepus, typical of Mammals :

Hair ;
Bones with diaphysis and epiphyses ;
Two condyles to the skull ;
Loss of coracoid ;
Tympanic bulla ;
Lower jaw composed of dentary only ;
Teeth heterodont and diphyodont ;
Articulation of dentary with squamosal ;
Conversion of articular and quadrate into malleus and incus ;
Diaphragm ;
Single left aortic arch ;

Non-nucleated red blood-corpuscles ;
Great expansion of cortex in cerebral hemispheres ;
Corpus callosum ;
Pons varolii ;
Turbinals ;
Cochlea spirally wound ;
Descent of testes into scrotal sac ;
Mammary glands ;
Uterus and placenta (allantoic) ;
Graafian follicles.

LITERATURE

BRADLEY, O. C. A Guide to the Dissection of the Dog. Longmans, Green, London, 1912.

HOWELL, A. B. Anatomy of the Woodrat. Baillière, Tindall and Cox, 1926.

MARSHALL, A. M., and HURST, C. A Junior Course in Practical Zoology. John Murray, London, 1920.

PART II

EMBRYOLOGICAL TYPES

CHAPTER XI

AMPHIOXUS

Fertilisation.—The egg is surrounded by a vitelline membrane secreted by itself, and contains yolk mostly aggregated at one (the vegetative) pole. It is freed from the ovary and makes its way to the outside via the atrium and atriopore, at a stage shortly after the extrusion of the first polar body. In the water a sperm penetrates into the egg, which then proceeds to give off the second polar body ; the egg and sperm pronuclei then fuse and fertilisation is effected. The second polar body marks the animal pole of the egg, and it persists throughout cleavage until the beginning of gastrulation, when it is possible to see that the future anterior end of the embryo arises at a point near the animal pole. Actually the axis of the egg (from animal to vegetative pole) makes an angle of $30°$ with the antero-posterior axis of the embryo. The egg-axis is determined in the ovary by the position of attachment of the egg to the germinal epithelium. The dorso-ventral median plane of symmetry of the embryo is marked by the point of entrance of the sperm.

Cleavage.—The cleavage of the egg is total or holoblastic, *i.e.* the amount of yolk present is insufficient to prevent cell-division, but the cells of the vegetative pole are larger than those at the animal pole. Up to the 8-cell stage, the cell divisions keep pace with one another, but after that they

become irregular. As a result of cleavage a ball of cells or morula is formed, and as the number of cells increases the ball becomes hollow. The central cavity is the blastocœl, surrounded by a single layer of cells which are smaller in the future anterior region of the embryo, and larger posteriorly. The embryo at this stage is a blastula.

Gastrulation.—The posterior side of the blastula, where
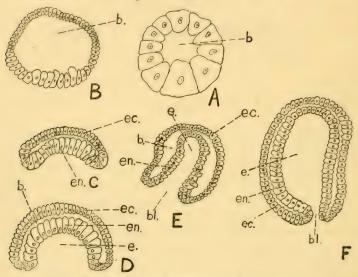
FIG. 68.—Amphioxus : early stages of development.

A, early blastula, showing the blastocœl (*b*) ; B, late blastula ; C, beginning of gastrulation, the ectoderm (*ec*) can now be distinguished from the endoderm (*en*) ; D, gastrula with primitive gut-cavity or enteron (*e*) ; E, late gastrula, showing the blastopore (*bl*) or mouth of the enteron ; F, stage in which growth in length has occurred as a result of the activity of the cells round the rim of the blastopore.

the cells are relatively larger, becomes flattened, and at one point (on the future dorsal side) actually tucked in beneath the more anterior smaller cells. In this way a lip is formed which soon extends right round the flattened region, which sinks in towards the centre of the blastula. This process of tucking-in is known as invagination, and the lip beneath which this takes place is the rim of the blastopore. At the same time as the flattened region is becoming invaginated, the

rim of the blastopore is growing over towards the future
posterior pole of the embryo, a process known as epiboly.
Between them, the processes of invagination and epiboly
result in the conversion of the hollow single-layered ball (the
blastula) into a double-layered hemispherical bowl. The
original cavity of the ball (the blastocœl) has been obliterated,
and the cavity of the bowl is the archenteron or primitive gut,
communicating with the exterior through the blastopore.
The embryo at this stage is known as a gastrula ; its outer
layer is the ectoderm which will give rise to the epidermis,
sense-organs, and nervous system ; its inner layer is the
endoderm which is destined to give rise to the lining of the
alimentary canal and its derivatives. The process of gastrula-
tion therefore entails the separation of these germ-layers.

The overgrowth of the rim of the blastopore or epiboly
continues as a result of the activity and division of its cells,
and produces an elongation of the embryo along its antero-
posterior axis. New cells are contributed to the ectoderm
outside and to the endoderm inside, and the blastopore
diminishes in diameter. The cells of the ectoderm develop
cilia, but the embryo is still enclosed within the vitelline
membrane.

Mesoderm, Nerve-tube, and Notochord.—The cells along
the middle line of the roof of the archenteron are destined to
form the notochord. On each side of them is a band of cells
which will give rise to the third germ-layer, or mesoderm.
The cells along the mid-dorsal line of the ectoderm form a
flat band which sinks in beneath the surface, and is grown over
by the ectoderm on each side, which rises up to form the
neural folds. This flat band is the neural plate ; it soon
becomes V-shaped in section, and the two arms of the V join
so as to give rise to a long tube running all the way along the
back just beneath the ectoderm : the nerve-tube. In front,
this tube is open at the neuropore, a place where the neural
folds have not met, and which is indicated by Kölliker's pit in
the adult. Behind, the neural folds rise up at the sides of
and behind the blastopore. When they meet, they roof over
the blastopore, which thus no longer communicates direct to

the exterior, but finds itself opening into the hind part of the nerve-tube. In this manner the neur-enteric canal is formed.
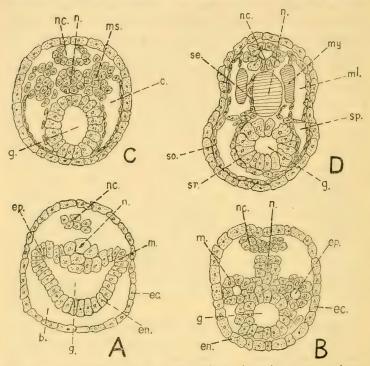
FIG. 69.—Amphioxus : transverse sections through young embryos, showing the origin of the notochord, nerve-cord, and mesoderm.

A, early stage showing the enterocœlic pouches (*ep*) still in communication with the gut-cavity (*g*) ; the roof of the gut is giving rise to the notochord (*n*) ; the nerve-cord (*nc*) although overgrown by the ectoderm (*ec*) has not yet formed a tube ; *b*, blastocœl ; *en*, endoderm ; *m*, mesoderm. B, later stage showing the enterocœlic pouches nipped off from the gut. C, stage showing the extension of the cœlom (*c*) between ectoderm and endoderm, the formation of mesodermal somites (*ms*) ; the notochord is separate from the gut, and the nerve-cord is rolling up. D, late stage, the nerve-cord is a tube, the cœlom is divided into myocœl (*ml*) dorsally and splanchnocœl (*sp*) ventrally, the inner wall of the latter cavity being the splanchnopleur (*sr*) and its outer wall the somatopleur (*so*). The inner wall of the myocœl is modified into a muscle-plate or myotome (*my*), and ventral to the latter is the sclerocœl (*se*).

The notochord rises up from the rest of the roof of the archenteron and forms a solid rod of cells extending all the

way down the body, just ventral to the nerve-tube. As the embryo grows in length, new cells are added on to the noto-chord rudiment from behind by the activity of the rim of the blastopore.

In each of the bands of cells which will give rise to the mesoderm, a longitudinal groove develops ; the groove opening widely into the cavity of the archenteron. The grooves deepen, and their front portions become separated from the more posterior region by a transverse partition on each side. These front portions become cut off from the archenteron altogether, and so a pair of mesodermal pouches are nipped off, each containing a portion of cœlomic cavity which has been in communication with the archenteron and is therefore called an enterocœl. This pair of pouches gives rise to the first pair of somites, and it must not be mistaken for the pair of anterior head-cavities or anterior gut-diverticula, which develops farther forward and at a later stage.

Behind the first pair of somites, the grooves become nipped off from the cavity of the archenteron anteriorly, while they continue to communicate with it posteriorly. This means that the mesoderm becomes separated from the wall of the archenteron progressively from in front backwards ; and it also becomes divided up by transverse partitions into somites from in front backwards. These posterior somites (from the second inclusive) differ from the first pair only in that the mesoderm from which they are formed becomes separated from the wall of the archenteron before being broken up into somites, whereas the first pair of somites is demarcated before losing connexion with the wall of the archenteron.

The mesoderm is therefore segmented very early, and each segmental block of mesoderm or somite is separated from the ones in front and behind by a septum. The somites in the anterior region are derived from tissue which was invaginated to form the original archenteron, and consequently they are said to be formed from " gastral " mesoderm. The more posterior somites owe their substance to the production of new cells by the rim of the blastopore as the embryo elongates, and such mesoderm is called peristomial. The difference between

these kinds is solely one of origin. After the separation of the mesodermal somites and of the notochord, the lateral edges of the endoderm grow over and meet to reform a roof over the gut-cavity.

The somites increase in size, and grow down between the gut and the ectoderm on each side. Eventually they meet beneath the gut and the wall separating them breaks down, so that the cœlomic cavity of each somite communicates with that of the corresponding somite on the opposite side of the body. The layer of cœlomic wall or epithelium which touches the endodermal wall of the gut is called the splanchnic layer, that touching the ectoderm of the surface of the body is the somatic layer. That part of the cœlomic wall which abuts against the nerve-tube and notochord on each side becomes thickened and gives rise to muscle-fibres forming the myotome : one myotome to each somite on each side. The more dorsal portions of the cœlomic cavity on each side, separating the myotome from the outer (or cutis) layer, are called the myocœls ; whereas the more ventral portion, into which the splanchnic layer suspends the gut from above, is the splanchnocœl. The myocœls become separated from the splanchnocœl of their somite by a horizontal partition. The myocœls retain their segmental arrangement, and remain separated by the septa from the myocœls of the somites in front and behind. The septa separating the splanchnocœls, however, break down, so that there is a continuous splanchnocœlic or perivisceral cavity from one end of the animal to the other.

The myotomes soon begin to show the V-shape characteristic of the adult, and the alternation in position between right and left sides.

In connexion with the mesoderm, there remain to be described a pair of pouches which become nipped off from the extreme front end of the wall of the gut. These are the anterior head-cavities, or anterior gut-diverticula. They arise symmetrically, but the right one soon occupies all the anterior region of the embryo in front of the 1st pair of myotomes, and becomes the head-cavity. The left anterior gut-diverticulum remains small, and eventually acquires an opening to

the outside at the bottom of an ectodermal inpushing called the preoral pit ; in the adult this opening is Hatschek's pit.

There is no mesenchyme in Amphioxus, and the connective tissue which surrounds the nerve-tube and notochord is derived from hollow ingrowths from the myocœls, forming the sclerocœls, the walls of which are the sclerotomes. The fin-ray boxes are also nipped off from the myocœls.

Portions of the myocœl persist in the adult between the myotomes and the connective tissue which surrounds them. Lastly, a downgrowth from each of the myocœls in the anterior
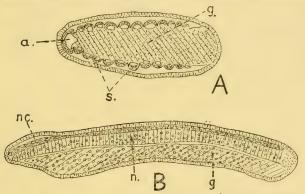
FIG. 70.—Amphioxus : young embryo and larva.

A, seen from above ; B, seen from the left side. *a*, anterior-gut diverticula ; *g*, gut ; *n*, notochord ; *nc*, nerve-cord ; *s*, mesodermal somites.

region of the body gives rise to the gonocœls, the walls of which (gonotomes) give rise to the gonads.

It is important to notice that the whole of the mesoderm in Amphioxus is segmented, and that this segmentation is retained everywhere except in the region of the splanchnocœl.

The Gut.—At the stage when there are two pairs of somites nipped off, the embryo hatches and emerges from the vitelline membrane as a larva. The gut is still a closed sac which communicates only with the nerve-tube, through the neurenteric canal. The mouth forms on the left side by a perforation between the ectoderm and the endoderm immediately underlying it. It is very asymmetrical and soon becomes a large opening bordered with cilia. In a similar way, the anus

forms as a perforation just beneath the neurenteric canal, which becomes closed and obliterated. Behind and dorsal to the anus the tail begins to grow back.

The cells lining the cavity of the gut become ciliated, and the splanchnic layer of cœlomic epithelium surrounding them gives rise to smooth muscle-fibres. The liver grows out as a diverticulum from the gut on the right side.

The origin of the structures of the pharynx is peculiar and complicated by the extraordinary asymmetry which the larva shows. A structure is formed by the downgrowth of a groove from the front of the floor of the gut, and is converted into a tube which eventually opens into the gut on the right side, and to the exterior a little to the left of the midventral line. This is the so-called club-shaped gland, which is regarded as the first gill-slit of the right side. The first gill-slit of the left side arises ventrally by a perforation between the gut and the ectoderm, and it moves up the *right* side of the body, opposite the mouth. Behind this slit, about a dozen more are formed ventrally, and likewise move up the *right* side, although they are destined to become the *left* gill-slits eventually. This series is known as the primary gill-slits. These slits correspond with the segmentation of the body at this stage ; but this correspondence is lost later on.

The definitive gill-slits of the *right* side, or secondary gill-slits, arise later than the primary, and above them on the right side to the number of eight. The most anterior secondary slit corresponds to the second primary slit, which is what would be expected if the club-shaped gland is really the first right gill-slit, corresponding to the first primary gill-slit.

In front of the club-shaped gland, there arises a thickening of the wall of the gut consisting of a strip of ciliated and glandular cells. This is the rudiment of the endostyle. It becomes V-shaped with the apex pointing backwards, and this apex grows backwards as a double strip along the wall of the pharynx on the right side above the primary slits and below the secondaries. It is as if the morphologically midventral line of the larva in the region of the pharynx were displaced up on to the right side. Soon the primary slits move round to
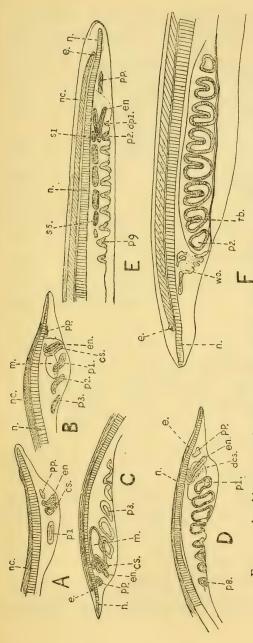
FIG. 71.—Amphioxus : a series of larvæ showing the development of the mouth, gill-slits and endostyle.

A, anterior end of a larva with one (the first) primary gill-slit (p 1) seen from the right side; cs, club-shaped gland; en, endostyle; nc, nerve-cord; pp, preoral pit. B, stage with three primary gill-slits (p 1, p 2, p 3), seen from the right side; the mouth (m) is seen through the body by transparency; n, notochord. C, stage with six primary gill-slits seen from the left side (the gill-slits are seen by transparency); e, eye-spot. D, stage with eight primary gill-slits, seen from the right side; the club-shaped gland is disappearing (dcs). E, stage in which the secondary gill-slits have appeared (s 1, s 5); the first primary gill-slit has disappeared (dp1) and the first secondary gill-slit is opposite the second primary; the endostyle is beginning to grow back between the primary and secondary gill-slits; the primary gill-slits are beginning to move down from the right side across the ventral side to the left side. F, critical stage with 8 pairs of gill-slits, symmetrically arranged ; tongue-bars (tb) are growing down and dividing all the gill-slits except the most anterior ; wo, wheel-organ.

the left side, the endostyle assumes a midventral position, and the secondary slits on the right side correspond more or less symmetrically with the primaries on the left. The first primary (left) gill-slit, and the club-shaped gland disappear, and the number of slits on each side is regulated to eight by the disappearance of the posterior primaries. After this stage, more and more gill-slits are formed symmetrically on both sides, and the segmental correspondence is lost.

All the gill-slits except the anterior pair become subdivided into two by the downgrowth of the secondary or tongue-bars. The perforation of the gill-slits naturally obliterates the cœlomic cavity at the place of perforation ; the cœlomic cavity is therefore restricted to the primary bars between the gill-slits, and to the dorsal cœlomic canals above and the subendostylar cœlom below. The tongue-bars have no cœlomic cavity, being downgrowths across the openings of the gill-slits. It is because of this difference in method of formation between the primary bars and the tongue-bars, that in the adult the former contain a portion of cœlomic cavity and the latter do not.

During the rearrangement of the gill-slits, the mouth moves round to the anterior end. Its aperture decreases in size as its margin grows-in all round to form the velum.

Folds of the skin give rise to the oral hood, in the roof of which the preoral pit finds itself. The latter flattens out, and its cells give rise to the wheel-organ, or ciliated organ of Müller.

The Atrium.—The atrium arises as a pair of ventral longitudinal folds, the metapleurs. These folds pass on each side of the region of the gill-slits, which come to be situated between them. From each fold, a median shelf or epipleur extends and meets its fellow from the opposite side, thus enclosing a part of the outside world as the cavity of the atrium. The cavity is completely closed in front ; behind it remains in communication with the exterior by the atriopore. The atrium is lined throughout by ectoderm.

The nephridia arise as little blind sacs eventually connecting with the exterior, at the top of each gill-slit (before the

formation of the tongue-bars, so that in the adult there is a
nephridium to every two gill-slits). Hatschek's nephridium
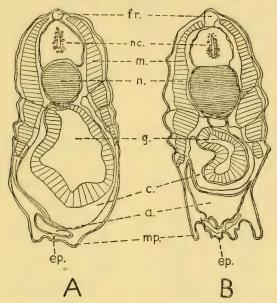
FIG. 72.—Amphioxus: transverse sections through larvæ showing the
development of the atrium.

A, early stage in which the cœlom (*c*) is still large, and the atrial cavity
(*a*) is small. B, later stage; *ep*, epipleural folds; *fr*, fin-ray box; *g*, gut;
m, myotome; *mp*, metapleural fold; *n*, notochord; *nc*, nerve-cord.

arises as a small tube near the preoral pit, but in the adult its
opening leads into the pharynx just behind the mouth.

Primitive features in the development of Amphioxus :

Cleavage total ;
Gastrulation with invagination ;
All mesoderm segmented ;
Enterocœlic pouches.

LITERATURE

KELLICOTT, W. E. Chordate Development. Henry Holt, New York.
1913.
MACBRIDE, E. W. Text-Book of Embryology, Vol. I. Macmillan,
London, 1914.

CHAPTER XII

DEVELOPMENT OF RANA (THE FROG)

Fertilisation.—The egg contains a large quantity of yolk, which is aggregated at the vegetative pole. This pole is light in colour when seen from outside, whereas the opposite animal pole, and indeed the whole animal hemisphere, is darkly pigmented. The nucleus is near the animal pole, which is determined in the ovary, probably by the relation of the developing egg to the little arteries and veins.

The egg is surrounded by three membranes. The inner vitelline membrane is secreted by the egg itself. Outside this is a tough membrane formed by the follicle-cells which surround the egg in the ovary. Outside this again is a coating layer of jelly which is secreted by the glands of the wall of the oviduct, as the egg passes down the latter on its way to the exterior.

At the time of spawning, the males climb on to the backs of the females, and as the latter extrude the eggs from their cloacal apertures, the former shed the sperm over them. Fertilisation thus takes place in the water outside the bodies of the animals. One polar body has been extruded before the egg is laid, the second polar body is pushed out after penetration of the sperm, and the egg- and sperm-pronuclei then fuse.

The jelly swells out on contact with the water, and after fertilisation the vitelline membrane becomes lifted off from the surface of the egg. The egg is then able to rotate, and comes to rest with the axis vertical, *i.e.* the vegetative pole with the heavy yolk is turned downwards.

The point of entrance of the sperm determines the median plane of symmetry of the future embryo, and, soon after fertilisation, this is indicated by the formation of the grey crescent

(due to the retreat of pigment into the egg) at the point dia-
metrically opposite to that at which the sperm entered.   The
egg can now be orientated with regard to the axes of the future
embryo.   The animal pole will become the head, and the
vegetative pole the tail ; the grey crescent marks the future
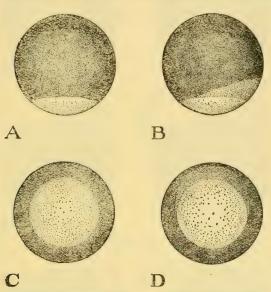
FIG. 73.—Egg of Rana temporaria (common frog) before and after fertilisa-
    tion, showing the formation of the grey crescent.   (From Jenkinson.)

A and B seen from the side ; C and D seen from below ; A and C
before and B and D after fertilisation.   The animal hemisphere is pig-
mented, the vegetative hemisphere is light in colour.

dorsal side, and the opposite side (where the sperm entered)
will be ventral.

Cleavage.—Cleavage in the frog's egg is total, but the size
of the various blastomeres is very unequal, owing to the large
quantity of yolk.   The cells at the vegetative pole are much
larger (and fewer in number) than those at the animal pole.
The blastocœl is small, and situated nearer to the animal than
to the vegetative pole.   The blastula is now a hollow ball,
but the hollow is small and its walls are several layers thick.

Gastrulation.—The cells of the animal hemisphere (which

are darkly pigmented) are relatively free from yolk, and therefore divide faster than the larger light-coloured yolk-laden
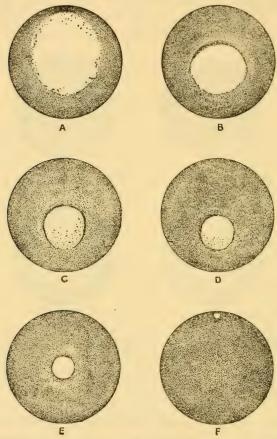
FIG. 74.—Formation and closure of the blastopore during gastrulation in Rana, seen from below. (From Jenkinson.)

In A the dorsal lip of the blastopore has just appeared ; in B the lateral lips have extended, and they almost meet in C ; in D the ventral lip of the blastopore (which is now a complete circle) has been formed ; and the diameter of the blastopore decreases in E and F.

cells of the vegetative hemisphere. One result of this is that the animal-pole cells begin to grow down over the lighter-coloured cells. This process starts by the formation of a lip
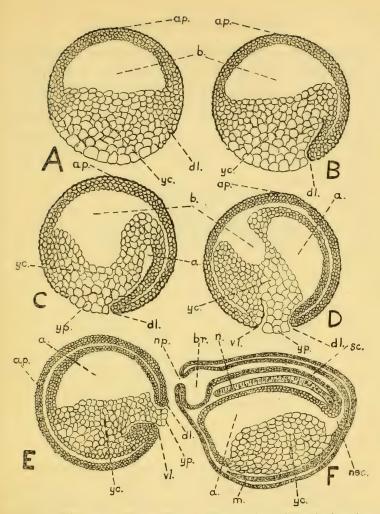
FIG. 75.—The process of gastrulation in Rana as shown by sagittal sections.

In A the dorsal lip of the blastopore has just appeared, and it is accentuated in B; in C a definite ingrowth is visible resulting in the formation of the archenteron: in D the ventral lip of the blastopore has appeared, and the yolk-containing cells of the vegetative hemisphere project through the now circular blastopore as the yolk-plug; in E the archenteron has extended greatly at the expense of the blastocœl, which in F is almost obliterated. During gastrulation the yolk-cells are heaped up on the ventral side of the archenteron, as a result of which the egg rotates until its original axis is more or less horizontal.

a, archenteron; *ap*, animal pole; *b*, blastocœl; *br*, brain; *dl*, dorsal lip of blastopore; *m*, mesoderm; *n*, notochord; *nec*, neurenteric canal; *np*, neuropore; *sc*, spinal cord: *vl*, ventral lip of blastopore; *yc*, yolk-cells: *yp*, yolk-plug.

of overgrowth in the centre of the grey crescent, forming the dorsal lip of the blastopore. Underneath this lip is a groove formed by the cells tucking in. The lips of the blastopore extend right and left from the site of its first appearance. At the same time the edge of overgrowth moves down towards the vegetative pole, and more and more of the lighter-coloured cells become covered over by the overgrowing darker ones.
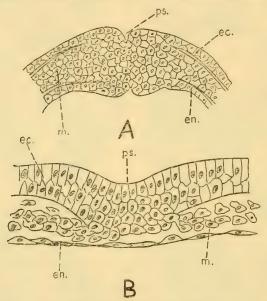
FIG. 76.—Transverse sections through the closed blastopore of Rana (A) and the primitive streak of Gallus (B).

The groove between the fused lips of the blastopore of Rana is the remnant of the blastopore, and corresponds to the primitive groove (*ps*) of Gallus. *ec*, ectoderm ; *en*, endoderm ; *m*, mesoderm ; all of which are continuous with one another at the rim of the blastopore or primitive streak.

Eventually the two horns of the lip of the blastopore meet on the ventral side, and the blastopore is then a closed ring, formed by overgrowing dark cells, and beneath which the tucking-in takes place. This tucking-in is most active on the dorsal side. The groove sinks deeper and deeper into the embryo, as the ingrowing cells push farther and farther forwards beneath the superficial layer. The groove represents the cavity of the

archenteron, largely filled up by the yolk-cells of the vegetative pole, which are visible inside the rim of the blastopore. The cavity of the blastocœl becomes reduced and obliterated as the cavity of the archenteron increases and gastrulation proceeds ; and the yolk-laden cells of the vegetative pole come to lie on the ventral side of the archenteron.

As the blastopore approaches the vegetative pole its diameter decreases, until when it reaches it, it is a small spherical hole with yolk-cells showing through as the so-called yolk-plug.

The processes of gastrulation therefore entail overgrowth or epiboly, and invagination ; but the invagination cannot take place simply as in Amphioxus owing to the large quantity of yolk present, and it is more in the nature of an ingrowth. At all events, the result of gastrulation is the conversion of the single-layered hollow ball (blastula) into a double-layered sac (gastrula) ; the outer layer (ectoderm) is formed of the cells of the animal hemisphere and those which have grown over, the inner layer (future endoderm and mesoderm) is formed of the cells which have grown in, and of the yolk-laden cells of the vegetative hemisphere. The latter form most of the ventral and the former most of the dorsal wall of the archenteron. The heaping up of the heavy yolk-cells at the ventral side causes the gastrula to rotate within its membranes, so that the former egg-axis lies more or less horizontal instead of vertical ; the ventral side now points downwards and the dorsal side upwards.

Mesoderm and Notochord.—The wall of the archenteron contains the cells which are destined to give rise to the notochord and to the mesoderm. A strip of cells running along the middle line of the roof of the archenteron is the rudiment of the notochord, and the mesoderm arises as a splitting off (or delamination) of a layer of cells from the remainder of the wall of the archenteron. This layer of mesoderm now separates the ectoderm from the endoderm in most parts of the embryo. Soon, a split arises in the mesoderm layer itself, dividing it into an inner splanchnic layer and an outer parietal or somatic layer. This split is of course the cœlomic cavity.

The notochord splits off as a solid rod from the surface of

N

the roof of the archenteron, which still forms a complete
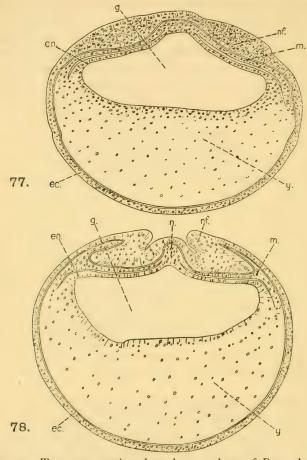
FIG. 77.—Transverse section through an embryo of Rana showing the separation of the mesoderm (*m*) from the endodermal wall (*en*) of the gut (*g*).

ec, ectoderm ; *y*, yolk-cells. Dorsally the ectoderm is thickening to form the neural folds (*nf*).

FIG. 78.—Transverse section through an embryo of Rana slightly older than the previous, showing the origin of the notochord (*n*) from the middle line of the roof of the gut. The neural folds (*nf*) have risen up and enclose a groove between them.

covering to the archenteric cavity. This delamination of the

mesoderm and notochord from the wall of the archenteron
begins in the anterior region of the embryo ; farther back they
are not distinct, and merge into the rim of the blastopore.
The rim of the blastopore may indeed be defined as the region
where the ectoderm, mesoderm, endoderm and notochord are
all in contact with a zone of actively growing cells, which
contributes new tissue to each layer.

The new mesoderm formed from the blastopore-rim is
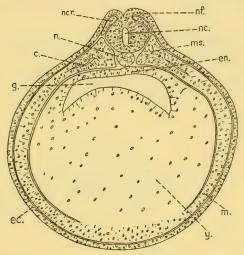
FIG. 79.—Transverse section through an embryo of Rana slightly older than
the previous, showing the complete separation of the notochord (*n*)
from the endodermal wall (*en*) of the gut (*g*).

The cœlom (*c*) has arisen as a split in the mesoderm (*m*), which forms a
somite (*ms*) on each side of the notochord. The neural folds (*nf*) have closed
over the groove converting it into the nerve-tube (*nc*), on each side of which
are the neural crests (*ncr*). *ec*, ectoderm ; *y*, yolk cells.

peristomial, that split off from the wall of the archenteron
farther forward, is called gastral mesoderm. Apart from their
method of formation, there is no difference between these two
kinds of mesodermal tissue.

This activity of the lip or rim of the blastopore is a continua-
tion of the process of epiboly, and its result is to produce an
elongation of the embryo. Eventually the blastopore becomes
oval and slit-like by the apposition to one another of its lateral

lips, and its former aperture is represented only by a short groove on the outer surface between these lips. This fact is of importance in connexion with the interpretation of development in higher forms. The activity of the cells of the blastopore-rim continues after the blastopore is closed, and leads to the outgrowth of the tail.

Nerve-tube.—The ectoderm along the middle line of the dorsal side thickens forming the neural plate. A pair of longitudinal ridges arise on each side of it, known as the neural
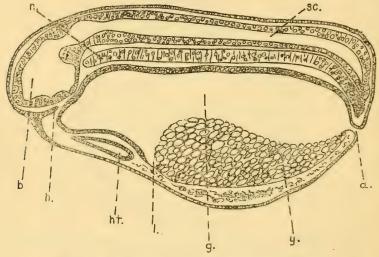
Fig. 80.—Sagittal section through an embryo of Rana.

a, anus ; *b*, brain ; *g*, gut ; *h*, hypophysis ; *ht*, heart ; *l*, liver ; *n*, notochord ; *sc*, nerve- (spinal) cord ; *y*, yolk-cells.

folds, and they enclose a groove between them. This groove is wider in front, where the brain will be, than behind, in the region of the future spinal cord. Posteriorly the neural folds embrace the blastopore. As the folds rise up they arch over the groove, which becomes converted into the nerve-tube. The nerve-tube communicates with the cavity of the gut posteriorly through the neurenteric canal and blastopore, which is still open at this stage.

The lateral part of the thickening which gave rise to the

neural plate does not get folded into the nerve-tube when the neural folds meet. It lies just to the side of the point of fusion of the neural folds, and forms the neural crest. The cells of the neural crest are destined to give rise to the afferent sensory nerve-cells, whose cell-bodies form the ganglia on the dorsal roots of the nerves, and to the sheaths of the nerves.

Segmentation.—The mesoderm on each side of the nerve-tube and notochord becomes thickened and divided into blocks, which are the somites from which the myotomes develop; they are metamerically segmented. This segmentation begins anteriorly and proceeds backwards; but it does not affect the more ventrally-situated mesoderm. Whereas the dorsal portion of the cœlomic cavity (on a level with the myotomes) is interrupted by transverse septa separating the mesodermal somites from the somites in front and behind, and consists of a number of myocœls equal to the number of somites, the ventral portion of the cœlomic cavity is continuous and un-interrupted by septa.

The segmented region of the mesoderm is called the verte-bral plate, the unsegmented portion is the lateral plate. Between each somite and the lateral plate immediately below it is a small region of segmented mesoderm known as the inter-mediate cell-mass, or nephrotome. From these structures the tubules of the kidneys will arise, and they are therefore also segmental. Eventually, the vertebral plate separates completely from the lateral plate, and the myotomes grow down in the body-wall lateral to the splanchnocœl to give rise to the muscles of the ventral surface, of the limbs, and the hypoglossal muscula-ture beneath the mouth.

Muscles formed from myotomes are always innervated by ventral nerve-roots, and as the myotomes are segmental, the ventral nerve-roots which grow freely out from the nerve-tube are segmental also. Further, the neural crest becomes sub-divided into pieces corresponding to the myotomes, these are the rudiments of the dorsal-root ganglia. The cells in these ganglia develop one process which grows into the nerve-tube, and another which pushes out to its destination in the body. These dorsal nerve-roots are therefore segmental also.

Median to the myotomes, cells are proliferated by the somites to form clouds of mesenchyme surrounding the nerve-tube and notochord. These cells are the sclerotomes (likewise segmental) from which later on the vertebræ are developed.

Another instance of segmentation will be seen in connexion
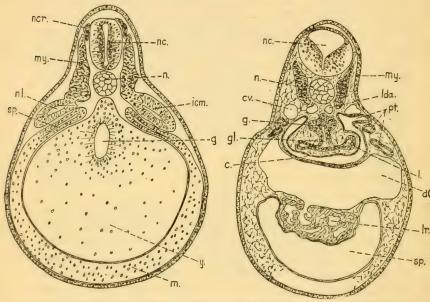
FIG. 81.—Transverse section through a young tadpole larva of Rana showing the origin of the kidneys.

FIG. 82.—Transverse section through a tadpole larva of Rana older than the previous, showing the formation of the kidneys and the lungs.

The section passes through the transverse septum across which the ductus Cuvieri lead from the cardinal veins to the heart. c, cœlom dorsal to the transverse septum ; cv, cardinal vein ; dC, ductus Cuvieri ; g, gut ; gl, glottis ; icm, intermediate cell-mass or nephrotome ; l, lung ; lda, lateral dorsal aorta ; lr, liver ; m, mesoderm ; my, myotome ; n, notochord ; nc, nerve-cord ; ncr, neural crest ; nl, nephrocœl ; pt, pronephric tubules ; sp, splanchnocœl ; y, yolk-cells.

with blood-vessels, which run transversely in the septa between adjacent segments. Although in the adult animal much of this segmentation is obscured and modified, it is important to note that in development, metameric segmentation is as well marked as in Amphioxus, except for the splanchnocœl.

As in invertebrates, segmentation begins with the mesoderm and extends to the other tissues.

The Gut.—The gut is a cavity with an accumulation of yolk-cells in the hinder part of its floor. This posterior region will become the intestine, and in front of it will develop the pharynx, œsophagus, and stomach. After the blastopore has closed, the anus breaks through near the same spot, as a result of the sinking in of an ectodermal pit (the proctodæum) till it meets the endoderm, and perforation ensuing. In a similar way, the mouth perforates in front, at the bottom of an ectodermal pit (the stomodæum).

Behind the mouth, in the region of what will be the pharynx, five pouches grow out on each side from the endoderm to the ectoderm. These are the rudiments of the visceral clefts. The first pair corresponds to the spiracles of the dogfish, but here they do not become perforated to the exterior. Their cavities persist as the Eustachian tubes. The remaining four pairs of pouches become the gill-slits, through which the pharynx communicates with the exterior.

Alternating with the visceral clefts are the visceral arches. The 1st or mandibular arch separates the mouth from the Eustachian tube (or hyomandibular cleft) ; the 2nd (or hyoid arch) is between the latter and the 1st gill-slit. The 6th visceral arch is behind the 4th gill-slit.

From the upper part of the 3rd, 4th, and 5th visceral arches, tufts grow out on each side which will become the external gills ; blood-vessels enter them, and they serve as the first respiratory organs. The dorsal part of the 1st gill-pouch on each side proliferates to form a body which is the rudiment of the thymus gland.

In the floor of the pharynx between the 2nd gill-slits, a downgrowth is formed, which ultimately loses its connexion with the pharynx and forms the thyroid gland. Close to the point of origin of the thyroid gland is an elevation which will eventually give rise to the tongue. A little farther back, also in the middle line of the floor of the pharynx, the rudiment of the larynx appears as a groove. This deepens into a tube remaining in connexion with the pharynx through the glottis.

From the posterior end of the larynx, the lungs develop as sacs stretching back parallel to the œsophagus on each side.
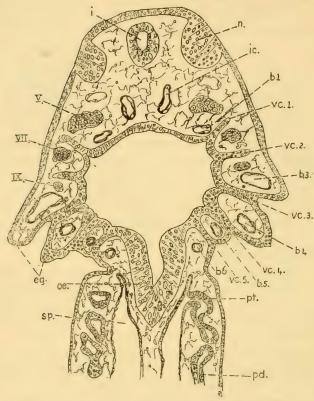
FIG. 83.—Horizontal section through the head of a tadpole of Rana, showing the formation of the visceral clefts (gill-slits).

b 1, *b* 3, *b* 4, *b* 5, *b* 6, blood-vessels running in the first, third, fourth, fifth, and sixth visceral arches (the vessels in the third and fourth arches will become the carotid and systemic arches respectively); *eg*, external gills; *i*, infundibulum (floor of the forebrain); *ic*, internal carotid artery; *n*, nasal sac; *oe*, œsophagus; *pd*, pronephric duct; *pt*, pronephric funnel; *sp*, splanchnocœl; *vc*, 1 to 5, first to fifth visceral cleft (the first will give rise to the Eustachian tube); V, VII, IX, branches of the trigeminal, facial, and glossopharyngeal nerve, running in the first, second, and third visceral arches respectively.

The liver arises as a ventral outgrowth of the floor of the gut, just in front of the mass of yolk-cells, and extending back

beneath them. Part of the cavity of this diverticulum becomes the gall-bladder, and the open connexion with the rest of the gut persists as the bile-duct. Close to this point, the pancreas arises as a number (three) of outgrowths, which remain connected with the gut by the pancreatic duct.

The cavity of the intestine is still small owing to the presence of the yolk-cells. After hatching, this yolk becomes absorbed and the intestine elongates very much, becoming coiled like a watchspring. Behind the intestine is the region of the gut which will become the rectum and cloaca. A downgrowth from the latter gives rise to the urinary bladder.

During this time, the right and left splanchnocœlic cavities have applied their outer (or somatic) layer to the body-wall, and their inner (or splanchnic) layer to the endoderm of the gut and all its derivatives. Ventrally, most of the membranes forming the separation between the right and left splanchnocœlic cavities break down ; but dorsally these walls persist forming the dorsal mesentery. This mesentery is composed of two closely apposed layers of cœlomic epithelium spreading round the gut and suspending it. It may be noticed, therefore, that the gut is not strictly in the cœlomic cavity at all ; it merely hangs in a fold of cœlomic epithelium which bulges into the cœlomic cavity. From the cells of this splanchnic layer are developed the smooth muscles of the stomach, intestine, and bladder.

Blood-vessels.—Beneath the floor of the gut, and between it and the underlying splanchnic layer of cœlomic epithelium, there are some scattered mesoderm-cells which become arranged in the form of a tube, or subintestinal vessel. In the region of the pharynx, this tube forms the endothelial lining of the heart. The cœlomic epithelium (splanchnic layer) surrounds this tube and suspends it as it were in a little mesentery of its own from the floor of the pharynx (the dorsal mesocardium). The musculature of the wall of the heart is derived from this layer of cœlomic epithelium, and that part of the splanchnocœl in which the heart finds itself is now called the pericardium. Later on, the various parts of the heart are differentiated. Posteriorly, the heart is continuous with two tubes, the vitelline

veins, which run from the yolk-cells and the rudiment of the liver.

The dorsal aorta arises as a pair of longitudinal vessels,
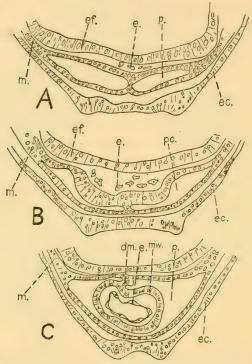
FIG. 84.—Transverse sections through embryos of Rana, showing the origin of the heart.

Only the ventral portion of the body is shown. A, early stage ; the cells which will give rise to the endothelial lining of the heart (*e*) are still scattered ; they lie between the endodermal floor of the gut (*ef*) and the mesoderm (*m*) ; the mesoderm contains right and left cœlomic cavities (*p*) still separated by a septum ; *ec*, ectoderm. B, later stage, the endothelial cells are beginning to arrange themselves, and the cœlomic epithelium underlying them becomes thickened and depressed. C, the endothelial lining of the heart is now a closed tube, and the cœlomic epithelium has folded round it forming its muscular wall (*mw*) ; it remains connected with the ordinary cœlomic epithelium above by the dorsal mesocardium (*dm*) ; beneath the heart, the septum between the right and left cœlomic cavities has disappeared so that the cœlom is continuous and is now known as the pericardium (*p, pc*).

close beneath the notochord. The two remain separate anteriorly, as the lateral dorsal aortæ and their prolongations

into the head, the internal carotids. Behind, they join and fuse together along the whole of the rest of the body, forming the single dorsal aorta.

Beneath the pharynx, the heart communicates forwards with the ventral aorta. In each of the 3rd to 6th visceral arches, between the gill-slits, a vessel appears which communicates below with the ventral aorta and above with the lateral dorsal aorta of its own side. In this way the series of pairs of aortic arches arise, alternating with the gill-slits. When the capillaries of the gills arise, they connect with the aortic arches which become interrupted. There are now afferent branchial arteries carrying blood from the ventral aorta to the gills, and efferent branchial arteries connecting the gills with the lateral dorsal aorta. Rudiments of aortic arches appear in the mandibular and hyoid arches.

The dorsal aorta sends arteries to the gut, which they reach by passing down between the two layers which form the dorsal mesentery.

The arteries become surrounded by coats of smooth muscle. Of the veins, the posterior cardinals arise near and parallel to the dorsal aorta. Their anterior prolongations are the anterior cardinal veins which run one on each side of the brain, and which, later on, contribute to the formation of the internal jugulars. At this period, the pericardial cavity is open posteriorly and communicates with the general periyisceral splanchnocœl. In the region of the heart, the splanchnic and somatic layers of the cœlomic epithelium approach one another and fuse, forming the lateral mesocardia which connect the gut-wall with the body-wall. This connexion of course interrupts the cœlomic cavity, and soon the pericardial cavity is completely shut off from the perivisceral cavity behind it. The partition formed by the lateral mesocardia is the transverse septum, and it is important in that it enables the cardinal veins, which are in the body-wall, to communicate via the ductus Cuvieri (or superior venæ cavæ) with the heart, which is of course situated in the gut-wall.

A third connexion between the heart and the veins of the body-wall is established by the formation of the inferior vena

cava, which runs down in the mesentery from the hinder region of the body.

As the liver develops, the vitelline veins (which are really that part of the subintestinal vessel which is behind the heart) undergo some modification. The hinder portion connects the intestine behind with the liver in front, forming the hepatic portal vein. The anterior portion connects the liver with the heart, and gives rise to the hepatic veins. The formation of the renal portal veins will be described in connexion with the kidneys.

The blood itself, or rather its red corpuscles, arise from structures known as blood-islands. These are formed from the layer of mesoderm which was split off from the floor of the original archenteric wall just beneath the mass of yolk-cells, behind the rudiment of the liver ; they are regions of rapid cell-proliferation. From here, the corpuscles enter the blood-vessels (which were previously empty) through the vitelline veins.

The Kidneys.—The kidneys are formed from the meso-dermal tissue situated at the junction between the myocœls and the splanchnocœl and which is known as the nephrotome or intermediate cell-mass. On each side a thickening appears in the region of the 2nd to 4th segments of the trunk of the embryo. This thickening extends back on each side as a rod of cells, between the outer layer of the splanchnocœl and the skin, to the cloaca. The thickening hollows out and a cavity appears which connects with the splanchnocœl by three openings surrounded with cilia. These are the cœlomic funnels. The rod of cells also becomes hollow and opens into the cloaca behind and connects with the cavity in front into which the cœlomic funnels open. There is now therefore a direct communication on each side between the cœlom and the cloaca. The three cœlomostomes and the little tubes or tubules into which they lead, together form the pronephros, which is the first and most anterior portion of the kidney to develop. The tube connecting it with the cloaca is the pronephric duct.

The tubules elongate and coil about, and as the posterior

cardinal veins develop just in this region, the tubules are as it were bathed in the venous spaces. At the same time, capillaries grow out from the dorsal aorta forming the glomus, which projects laterally towards the openings of the cœlomostomes from the mesentery, on each side.

The pronephros is the functional kidney of the embryo and early larva. Later on, however, it degenerates, and its function is taken over by another set of cœlomic funnels and tubules, which together form the mesonephros.

The mesonephros is developed from the nephrotomes of half a dozen segments, some little distance behind the pronephros. Cavities hollow out in the nephrotomes, and these connect with the splanchnocœl by cœlomic ciliated funnels, and by coiled tubules with the pronephric duct. The latter loses connexion with the degenerating pronephros, and, after being tapped so to speak by the mesonephric tubules, it is known as the mesonephric or Wolffian duct.

The tubules multiply by branching, and form little chambers or Bowman's capsules which lose their connexion with the cœlomic funnels. Arterioles from the dorsal aorta and venules from the posterior cardinal veins form little bunches of capillaries which project into the capsules forming glomeruli. Capsule and glomerulus together form a Malpighian corpuscle. That portion of the posterior cardinal veins which lies behind the mesonephros becomes the renal portal vein, which brings blood from the posterior regions of the body to the kidneys. The mesonephros is the functional kidney of the adult. It extracts excretory matter from the blood stream and passes it down the Wolffian duct to the cloaca, which develops a ventral outpushing, the urinary bladder.

Reproductive Organs.—The gonads arise as ridges which project into the splanchnocœl on each side of the dorsal mesentery. The germ-cells which they contain are derived partly from the cœlomic epithelium in situ, and partly from cells which have migrated up in the mesentery from the yolkmass. For a long time the sexes are indistinguishable. Strings of germ-cells grow in, away from the surface of the gonads, forming the genital strands. In embryos which are

going to be males, these hollow out forming the seminiferous tubules which become connected with the cavities of the tubules of the mesonephros.   In this way the vasa efferentia are formed, and they may be regarded as persistent cœlomic funnels, placing the testis in communication with the exterior (via the cloaca).   The sperms therefore make their way through the tubules of the mesonephros, down the Wolffian duct or vas deferens as it can also be called, to the exterior.

The Müllerian ducts develop as grooves in the roof of the splanchnocœl at the side of the gonads.   The sides of the groove grow over, and convert it into a tube which opens into the cœlomic cavity in front (near the place where the pronephric funnels were), and grows back to open into the cloaca behind. In males the Müllerian ducts disappear.

The kidneys and gonoducts are mesodermal all the way, and are really cœlomoducts, whose primitive function is probably to connect the cœlomic cavity with the exterior and so allow the germ-cells to escape.   They take on the function of excretion as a result of the proximity of the tubules to the blood-vessels.

On the other hand, the nephridia have excretion as their primitive function ; they do not occur in Chordate animals other than Amphioxus.

Paired Sense-organs and Brain.—The eyes make their appearance as outpushings from the sides of the brain, forming the optic vesicles.   Each of these vesicles grows towards the overlying ectoderm, and becomes an optic cup, with the concave side turned outwards.   The lens is formed from the ectoderm overlying the optic cup, as a little vesicle which soon becomes nipped off, and sinks into place at the mouth of the cup.   While the cup is really part of the brain, the lens is part of the epidermis, but both are ectodermal.   The outer lining of the cup forms the pigment or tapetum layer, the inner lining of the cup differentiates to form the sensitive retina, and it is inverted since the nerve-fibres run between the sensitive cells and the seen object (see p. 24).   Outside the tapetum, mesodermal tissue gives rise to the choroid and sclerotic (including the transparent cornea) layers, just as round

the brain it forms the pia mater (vascular) and dura mater (protective). The eye-muscles arise from mesodermal tissue which represents the three first somites of the head.

The ears arise as a pair of ingrowths from the ectoderm behind the eyes, forming the auditory vesicles. Their connexion with the ectoderm becomes severed and the remains
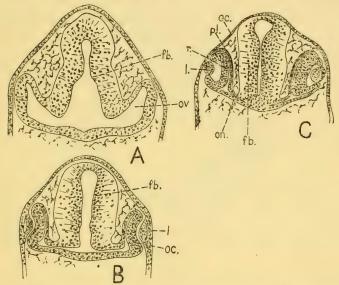
FIG. 85.—Transverse sections through the head of embryos of Rana showing the development of the eyes.

A, early stage, in which the optic vesicles (*ov*) have been pushed out on each side from the forebrain (*fb*). B, the outer walls of the optic vesicles have been pushed in, converting them into optic cups (*oc*); the lens (*l*) arises opposite the mouth of the optic cup from the ectoderm (*ec*). C, late stage; the cavity of the optic vesicle has been almost obliterated, the lateral layer of the optic cup is the retina (*r*) and the median layer is the pigment layer (*pl*), the stalk attaching the optic cup to the forebrain is the optic nerve (*on*), the lens has become detached from the ectoderm.

of the connecting stalk is the ductus endolymphaticus. Each vesicle now forms a closed sac at the side of the hinder part of the brain, and above the tympanic cavity, which develops as an expansion of the hyomandibular visceral pouch (Eustachian tube). From the dorsal portion of each vesicle three shelf-like projections are formed. The centre of each shelf becomes

perforated, converting the shelf into a half-ring. In this way the semicircular canals are formed. The cavity of the auditory sac contains endolymph. Between the wall of the sac and the capsule of connective tissue which surrounds it, is the perilymph. The capsule eventually becomes cartilaginous, and later on, bony; but certain apertures are left. One of
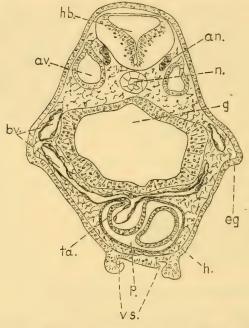
FIG. 86.—Transverse section through an embryo of Rana showing the formation of the ears.

an, auditory nerve; *av*, auditory vesicle; *bv*, blood-vessels running in the visceral arches; *eg*, external gills; *g*, gut; *h*, heart; *hb*, hindbrain; *n*, notochord; *p*, pericardium; *ta*, truncus arteriosus; *vs*, ventral sucker.

these is the fenestra rotunda, and another is the fenestra ovalis on to which the base of the columella auris fits. The outer end of the columella auris is applied to the thin lateral wall of the tympanic cavity which forms the tympanic membrane.

It may be mentioned here that, remarkable as it may seem, the ears are responsible for the formation of the so-called calcigerous glands, or glands of Schwammerdamm. These glands

are conspicuous objects in the trunk of the frog, lying on each side of the vertebræ, close to the points of exit of the spinal nerves. Diverticula from the auditory vesicles grow into the brain-case, and back down the canal formed by the vertebræ and which contains the spinal cord. From here, the diverticula of the auditory vesicle emerge through the foramina for the spinal nerves and give rise to the glands of Schwammerdamm (function unknown).

The olfactory organs arise as a pair of thickenings of the ectoderm, which sink in to form pits just above the mouth. The cells lining these pits will give rise to the olfactory epithelium. Behind, the pits reach the roof of the mouth and break through forming the internal nostrils.

The various regions of the brain are roughly marked out even before the neural folds have closed over. The definitive form of the brain is soon reached by means of foldings and thickenings of its walls in certain places.

A median ectodermal inpushing arises from the epidermis of the front of the head, just above the mouth. This is the hypophysis which grows back beneath the floor of the fore-brain until it meets and fuses with the infundibular downgrowth from the brain. Hypophysis and infundibulum together form the pituitary body.

Placodes and Lateral-line Organs.—The dorsal nerves and ganglia in the region of the trunk consist of nerve-cells which have been derived entirely from the neural crests. In the region of the head, the dorsal nerve-ganglia are derived not only from the neural crest, but also from thickenings of the ectoderm at the sides of the head called placodes. Placodes are proliferations of the deeper layers of the epidermis which contribute cells to the underlying ganglia. The profundus, trigeminal, facial, glossopharyngeal and vagus ganglia all derive cells from the epidermis in this way, and the auditory nerve is formed from the placode which invaginates with the auditory sac. Indeed, the thickenings of the epidermis which later become pushed in to form the olfactory sacs, the lens, and the auditory sacs, may themselves be regarded as placodes.

There are two kinds of placodes : an upper row of dorso-lateral placodes which give rise to the lateral-line sense-organs and to the nerve-cells whose fibres innervate them ; a lower row of epibranchial placodes situated at the dorsal ends of the visceral slits, and which give rise to the nerve-cells whose fibres innervate the sense-organs of taste.

Sympathetic System and Adrenals.—The dorsal nerve-root, formed by fibres which have grown out from cells in the dorsal-root ganglion, and the ventral nerve-root which has grown out from the spinal cord, join to form a mixed nerve. Certain cells migrate out from the spinal cord, and, leaving the mixed nerve, make for the side of the dorsal aorta where they form the sympathetic ganglia. These ganglia remain con-nected with the mixed nerve by the rami communicantes. The sympathetic ganglia are, like the mixed spinal nerves, seg-mentally arranged. They soon become connected by fibres running to the (sympathetic) ganglia in front and behind them forming the sympathetic trunks. From the sympathetic ganglia, " postganglionic " fibres are distributed to the smooth muscles of the gut, oviducts, and blood-vessels. Other cells migrate out from the sympathetic ganglia, and give rise to the medulla of the adrenal bodies. The cortex of these bodies is derived from the cœlomic epithelium in the region between the mesonephric kidneys.

It may be mentioned that cells migrate out from the hind-brain along the vagus and eventually come to lie on the surface of the heart and gut, forming part of the parasympathetic system.

Skeleton.—The vertebral column arises in the form of paired cartilages beside the notochord, derived from the sclerotomes. Each vertebra arises opposite the septum separating two segments ; the vertebræ are therefore inter-segmental in position.

In the skull, paired trabeculæ arise as struts underlying the forebrain, and, behind them, paired parachordals flank the notochord. The pterygo-quadrate or skeleton of the upper jaw arises early, and fuses on to the remainder of the skull by its ascending process. The auditory sac becomes surrounded

by a cartilaginous capsule which gets attached to the para-chordals on each side. Similarly, nasal capsules surround the olfactory sacs and become attached to the front of the trabeculæ. The floor of the skull is established in this way, and the sides and roof develop later.

In each of the visceral arches separating the gill-slits, cartilaginous struts develop. In the mandibular arch, these are the pterygo-quadrate, and Meckel's cartilage which forms the lower jaw. The dorsal portion of the skeleton of the 2nd or hyoid arch forms the columella auris. The cartilages of the remainder of the arches eventually form a plate beneath the floor of the mouth and pharynx, and which by raising and lowering this floor assists in the process of respiration. The skeleton of the limbs and girdles does not appear until a late stage of development.

This cartilaginous skeleton is later on partly replaced by cartilage-bones, and in addition, membrane-bones are developed.

Teeth arise late. In their formation, an ingrowth of ecto-derm takes place inside the margin of the mouth, forming the enamel-organs of the teeth. These secrete a cap of enamel beneath which the mesodermal cells produce the body of the tooth which is composed of dentine. Eventually the tooth is pushed up through the surface of the mouth and its base is attached to the bone of the jaw.

Externals.—By the time that differentiation and the forma-tion of organs have proceeded as far as has just been described, the embryo emerges from its membranes and hatches into a free-swimming larva which is familiarly known as the tadpole. Its ectoderm is ciliated, and just beneath the mouth it has a V-shaped sucker by means of which it can attach itself to objects. Its tail elongates and develops dorsal and ventral extensions or fins, which make it a very efficient organ for swimming. Its food consists of vegetable matter, its stock of yolk being by now used up. Food is seized by the edges of the mouth or lips which are assisted by horny epidermal teeth, which have of course nothing to do with the true teeth.

From the sides of the head, folds grow back which cover

over the gill-slits. The external gills disappear, and so-called internal gills develop in the walls of the gill-slits and subserve the function of respiration. The folds just mentioned form the operculum, which leaves only a small hole on the left side through which the water which passes through the gill-slits may escape.

The organisation of the larva is just like that of a fish, and there is little indication of the frog into which it will develop. The changes which take place in the conversion of the tadpole into the frog are known as metamorphosis.

Metamorphosis. — The chief differences between the organisation of the tadpole and that of the frog concerns the limbs, lungs and pulmonary respiration, intestine, tongue, and tail.

The limbs arise as buds in tadpoles about half an inch long, and muscles grow into them from the myotomes. The buds of the forelimbs are, however, concealed beneath the operculum, and are therefore invisible. Those of the hind-limbs are situated at the base of the tail, on each side of the cloaca. In time, the fore limbs grow out through the operculum, making use of the opening on the left side and making a new one on the right. Soon the limbs become visibly jointed and the toes appear.

Meanwhile, the lungs are developing, and to each of them there runs a blood-vessel which is formed as a branch from the efferent artery of the last or 6th arch. This vessel is the rudiment of the pulmonary artery. From time to time, the tadpole takes in a gulp of air at the surface of the water and fills its lungs. A certain amount of oxygenation of the blood now begins to take place in the lungs, and the gill-circulation becomes reduced by the establishment of direct connexions between the afferent and efferent branchial arteries. The gills therefore become " short-circuited," and left out of the circulation gradually as more and more of the blood goes to the lungs to be oxygenated, and returns to the heart by the pulmonary veins. The now continuous vessel in the 3rd visceral arch becomes the carotid, that in the 4th becomes the systemic arch, that in the 5th disappears, and the 6th as

already seen becomes the pulmonary. The lateral dorsal aorta between the dorsal ends of the carotid and systemic arches (the ductus caroticus) disappears, as also does the connexion between the pulmonary artery and the lateral dorsal aorta (ductus arteriosus, or Botalli). After this change, the organism is perfectly adapted to breathe in air after the manner of land-animals.

The gills disappear ; the gill-slits close up ; the animal ceases feeding, and the horny teeth drop off. The mouth becomes wider and its angle moves farther back. The tongue develops, and the eyes become more prominent and bulge out from the top of the head. The lateral-line organs disappear and the skin is shed. Glands appear which will keep it moist on land. Internally, great changes take place in the intestine, which loses its watchspring-like coils, and becomes relatively much shorter. This is an adaptation to the carnivorous habits of the frog, for less surface is required for the digestion of a meal of animal food. Lastly, the tail becomes reduced and finally completely absorbed, its debris being ingested by wandering white blood-corpuscles, or phagocytes.

This astonishing and comparatively rapid change is brought about by the secretion of the thyroid gland, which has been increasing until it reaches a size sufficient to " pull the trigger " of metamorphosis. During the process of change the weight of the body actually decreases, but after coming out on land and recommencing to feed, the size of the young frog increases.

LITERATURE

JENKINSON, J. W. Vertebrate Embryology. Oxford, at the Clarendon Press, 1913.

KELLICOTT, W. E. Chordate Development. Henry Holt, New York, 1913.

MORGAN, T. H. The Development of the Frog's Egg. Macmillan, New York, 1897.

CHAPTER XIII

DEVELOPMENT OF GALLUS (THE CHICK)

Fertilisation.—The true egg of the hen is all that is contained within the membrane that just surrounds the yolk. It is therefore of relatively enormous size for a single cell, and this is due to the very large quantity of yolk which it contains. The pure protoplasm, of which there is comparatively little, is situated at the animal pole, which is the point at which the follicle-stalk is attached to the ovary. The egg is surrounded by the vitelline membrane which it has secreted and which thickens to form the zona radiata, perforated by numerous holes through which nutriment is passed to the egg from the surrounding follicle-cells. This is a primary membrane. The egg bursts out of its follicle into the cœlom, and the follicle is left behind. There is therefore no secondary membrane. The nucleus has grown to a very large size, and the first polar body is formed inside the mouth of the oviduct, which as it were grasps the follicle containing the egg before the latter has left the ovary (or been " ovulated ").

Sperms are introduced into the cloaca of the female during copulation, and they make their way up to the top of the oviduct where several of them penetrate an egg. After the second polar body has been formed, one of these sperm-nuclei fuses with that of the egg, and the other sperms degenerate.

The fertilised egg then begins to develop, and passes down the oviduct. The walls of the latter secrete the tertiary membranes round it in the form of a layer of albumen, an inner and an outer shell-membrane, a hard shell formed by depositing lime salts, and this in many birds is coated with a layer of

pigment which gives the " egg " its characteristic colour and pattern.

The egg goes down the oviduct with its axis transverse to the long axis of the oviduct, and it is rotated as it descends, with the result that the denser albumen at the two ends, in the axis of rotation, is spirally wound and forms the chalazæ.
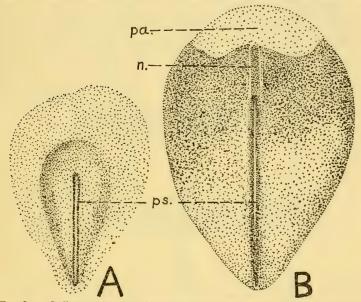
FIG. 87.—Gallus : view of the blastoderm of a hen's egg.   (After Jenkinson.)
A after 12 hours', B after 18 hours' incubation, as seen by transmitted light.   *n*, notochord ; *pa*, proamnion ; *ps*, primitive streak.

At the blunt end of the egg, the two shell-membranes are separated by a space full of air, the air-chamber.

Cleavage.—Soon after fertilisation, the process of cleavage begins ; its early stages therefore take place while the egg is descending the oviduct, and it has proceeded some way when the egg is laid. The amount of yolk compared with that of protoplasm is so big that cleavage is incomplete, or meroblastic. While the small quantity of protoplasm at the animal pole divides into a number of cells arranged like a small disc or blastoderm on the top of the yolk, the latter is

undivided. The margin of the blastoderm merges with the yolk round it, forming the periblast; and beneath the blastoderm is a cavity, the blastocœl, which separates it from the underlying yolk. This stage, when the blastoderm is but a single layer (though of many cells), represents the blastula of Amphioxus and the frog.

Gastrulation.—A layer of cells becomes split off from the under side of the blastoderm, between it and the underlying yolk. This layer soon extends over the under surface of the blastoderm and is known as the " lower layer," or secondary endoderm. It is continuous with the upper layer all round
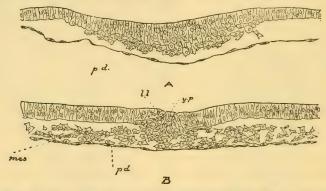
Fig. 88.—Gallus : transverse sections through the primitive streak of the blastoderm of a hen's egg. (From Jenkinson.)

A after 10 hours', B, after 15 hours' incubation. *ll*, lateral portion of the primitive streak corresponding to the lateral lip of the blastopore (*cf.* Fig. 76) ; *mes*, mesoderm ; *pd*, endoderm ; *yp*, primitive groove.
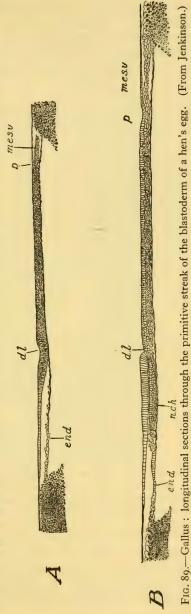
the margin, and, like it, merges into the periblast. The blastoderm extends gradually over the yolk, and in so doing it forms a margin of overgrowth. In this region, all round the edge of the blastoderm (which is called the germ-wall), the protoplasm is thicker than in the centre. When therefore a blastoderm is looked at by transparency, two zones are distinguishable. Centrally there is a relatively clear area pellucida; and round the edge is a denser area opaca. The egg is usually at this stage when it is laid, some twenty-four hours after fertilisation.

A thickening of the upper layer of the blastoderm appears in the centre of the area pellucida, in the form of a straight band stretching at right angles to the line passing through the pointed to the blunt end of the "egg." This is the primitive streak, the first differentiation of the embryo, which will be formed along its axis. When an observer holds an egg in front of him with the blunt end to the left, the axis of the embryo will therefore run straight in front of him, and the embryo is so orientated that its head is away from the observer, and its tail towards him.

Running along the middle line of the primitive streak is a shallow groove on the surface, the primitive groove, which runs into a small depression at the front end of the primitive streak known as the primitive pit. Immediately in front of the primitive pit is a slight rise, forming the so-called primitive knot. Now the primitive knot

Fig. 89.—Gallus : longitudinal sections through the primitive streak of the blastoderm of a hen's egg. (From Jenkinson.) A after 10 hours', B after 15 hours' incubation. *dl*, primitive pit, corresponding to the dorsal lip of the blastopore ; *end*, endoderm ; *mesv*, mesoderm ; *nch*, notochord ; *p*, hind end of the primitive streak.

is the dorsal lip of the blastopore, and the primitive streak represents the lateral lips of the blastopore, fused together along their whole length. All that is left of the aperture of the blastopore is the primitive pit and the primitive groove. This is the condition of the blastopore of the frog after its
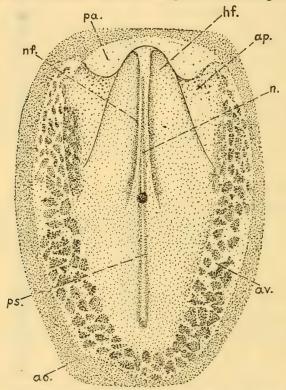
FIG. 90.—Gallus : view of the blastoderm of a hen's egg after 20 hours' incubation, as seen by transmitted light. (After Jenkinson.)

ao, area opaca ; *ap*, area pellucida ; *av*, area vasculosa ; *hf*, head-fold ; *n*, notochord ; *nf*, neural fold ; *pa*, proamnion ; *ps*, primitive streak.

aperture has become slit-like and closed by the apposition of its lateral lips. The chick therefore starts straight away from the condition reached in the frog at the close of gastrulation.

The primitive streak, like the lip of a blastopore which it is, is a region of cell-proliferation, and it gives rise to mesoderm-

cells which grow out laterally between the upper and lower layers. The primitive knot produces tissue which gets pushed forwards underneath the upper layer in the middle line, and
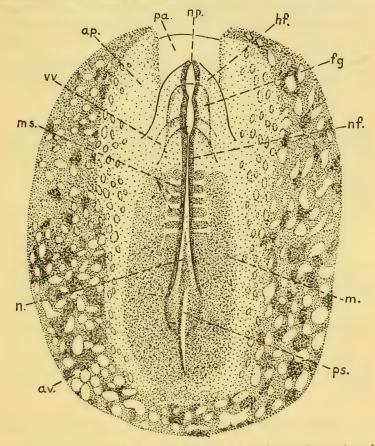
Fig. 91.—Gallus : view of the blastoderm of a hen's egg after 24 hours' incubation, as seen by transmitted light. (After Jenkinson.)

fg, foregut ; *m*, mesoderm ; *ms*, mesodermal somites ; *np*, neuropore ; *vv*, vitelline vein. Other letters as Fig. 90.

gives rise to the notochord. During development the primitive streak moves back along the blastoderm, leaving in front of it a trail of cells destined to become notochord, and on each side

(peristomial) mesoderm. At the extreme front end of the embryo, anterior to the region of the midbrain which is the farthest spot reached by the proliferation of the primitive pit and streak, a certain amount of mesoderm and the front end of the notochord are formed by splitting off from the lower layer. As in Amphioxus and the frog, therefore, the most anterior part of the mesoderm (gastral) and of the notochord are formed from the endoderm by delamination or splitting,
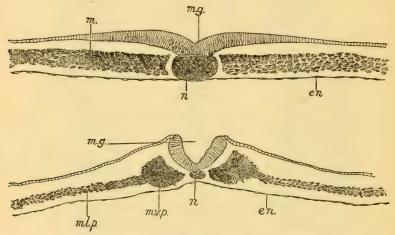
FIG. 92.—Gallus : transverse sections through the blastoderm of a hen's egg after 24 hours' incubation. (From Jenkinson.)

A, through the posterior ; B, through the anterior region of the embryo. *en*, endoderm ; *m*, mesoderm ; *mg*, neural groove ; *mlp*, unsegmented meso-derm of the lateral plate ; *mvp*, segmented mesoderm (somites) of the vertebral plate ; *n*, notochord. The posterior region of the embryo is at a less advanced stage of development than the anterior region.

while farther back they are formed as a result of the activity of the cells of the lips of the blastopore (primitive streak).

The upper layer of the blastoderm may now be called ectoderm, the lower layer endoderm, and the mesoderm extends out to the side between them. Gastrulation in the chick therefore does not involve invagination. The endoderm is formed precociously, probably so as to assist in digesting the enormous quantity of yolk.

Head-fold.—A very important thing to notice is that the

embryo in the chick will develop from only a part of the egg and blastoderm. The remainder will give rise to the membranes outside the embryo. At first, all that exists of the embryo proper is the middle line of its back represented by the primitive streak. Its sides are formed as this streak-
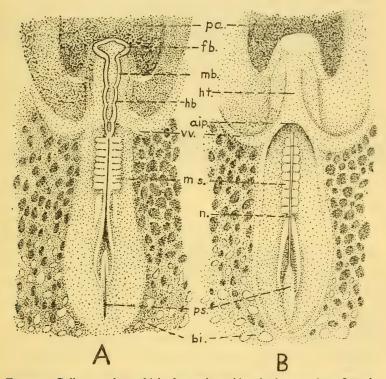

FIG. 93.—Gallus : embryo chick after 30 hours' incubation seen by reflected light A from the dorsal, B from the ventral side. (After Jenkinson.)

aip, anterior intestinal portal ; *bi*, blood-islands ; *fb*, forebrain ; *hb*, hind brain ; *ht*, heart ; *mb*, midbrain. Other letters as Figs. 90 and 91.

region rises and becomes folded up from the surface of the blastoderm around it. This process begins in front with the formation of the head-fold ; by this means the ectoderm, notochord, mesoderm, and endoderm are lifted off from the surface of the underlying yolk, and a cavity appears between

the latter and the endoderm which represents the foregut-region of the enteron. As yet there is no floor to the gut, nor is the ventral side of the embryo formed at all. The mesoderm, lying on each side of the notochord becomes segmented into somites. That part which is nearest to the notochord will produce the myotomes; farther laterally, a split arises in the mesoderm which becomes the cœlomic cavity, and which separates a somatic layer of mesoderm closely applied to the ectoderm from a splanchnic layer which is similarly applied to the endoderm. The ectoderm, mesoderm, and endoderm extends to the side far beyond the limits of the
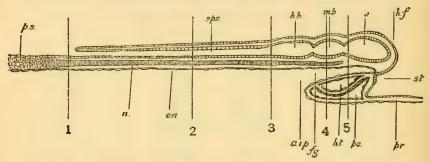
Fig. 94.—Gallus : longitudinal section through the head-region of an embryo chick after 30 hours' incubation. (From Jenkinson.)

aip, anterior intestinal portal ; *en*, endoderm ; *pc*, pericardium ; *pr*, proamnion ; *spc*, spinal cord ; *st*, stomodæum. Other letters as Figs. 90, 91, and 93. The lines marked 1 to 5 indicate the planes of the transverse sections shown in Figs. 95 and 96.

embryo, and so it comes about that the cœlomic cavity of the embryo is perfectly continuous with the " extra-embryonic " cœlom. As this extra-embryonic splanchnic mesoderm spreads out, blood-islands develop between it and the endoderm. This is seen in blastoderms observed by transparency as the spreading of an area vasculosa over the area pellucida. Eventually this area vasculosa spreads over most of the blastoderm up to the germ-wall, except for a region immediately in front of the head-fold which is known as the proamnion. The peripheral extent of the area vasculosa is marked by a blood-vessel, the sinus terminalis.

Nerve-tube.—The neural plate develops as a thickening

of the ectoderm along the axis of the embryo, in front of the primitive knot. At its sides are the neural folds which rise up and meet forming the neural tube. The first part of the neural tube to form is the brain, which is clearly marked out
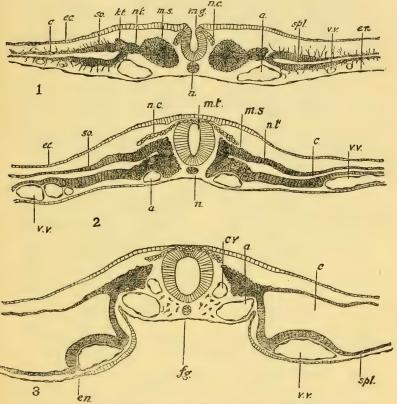
FIG. 95.—Transverse sections through an embryo chick after 30 hours' incubation. (From Jenkinson.)

Taken in the planes shown by lines 1, 2, and 3 on Fig. 94. *l* is posterior. For lettering see Fig. 96.

into the regions which will become the fore-, mid-, and hind-brain. As the primitive knot and streak move back, the neural folds follow them and cover up the spots which they formerly occupied, and so the neural tube comes to be formed immediately above the notochord. On each side of the neural

tube, the neural crests come into existence, as in the frog.
Even at very early stages, the rudiments of the eyes may be
seen as outpushings to each side from the fore-brain. In
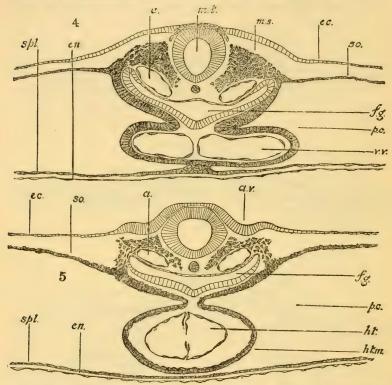
FIG. 96.—Transverse sections through an embryo chick after 30 hours'
incubation. (From Jenkinson.)

Taken in the planes shown by lines 4 and 5 on Fig. 94. 5 is anterior.
a, lateral dorsal aorta ; *av*, auditory vesicle ; *c*, cœlom ; *cv*, cardinal vein ;
ec, ectoderm ; *en*, endoderm ; *fg*, foregut ; *ht*, heart endothelium ; *htm*, mus-
cular wall of heart ; *kt*, kidney tubule ; *mg*, neural groove ; *ms*, mesodermal
somite ; *mt*, nerve-tube ; *n*, notochord ; *nc*, neural crest ; *nt*, nephrotome ;
pc, pericardium ; *so*, somatopleur ; *spl*, splanchnopleur ; *vv*, vitelline vein.

front, the neural tube remains open for a time at the neuropore,
which is situated at that part of the brain destined to become
the lamina terminalis.

Amnion.—In front of the head of the embryo, a fold rises
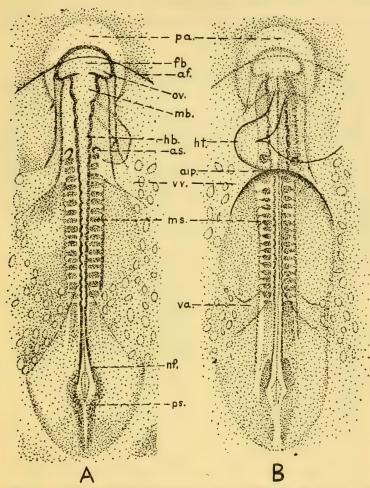
FIG. 97.—Gallus : embryo chick after 36 hours' incubation seen by transmitted light, A from the dorsal, B from the ventral side. (After Jenkinson.)

The heart is beginning to bend to the right, and the amniotic folds are covering over the head. *af*, amniotic fold ; *as*, auditory sac ; *ov*, optic vesicle ; *va*, vitelline artery. Other letters as Figs. 90, 91, and 93.

up from the extra-embryonic part of the blastoderm. This fold extends backwards, and soon covers over the head. It now continues growing backwards by the upgrowth of folds

P

on each side of the embryo, and soon covers over the latter completely, much in the same manner as the neural folds
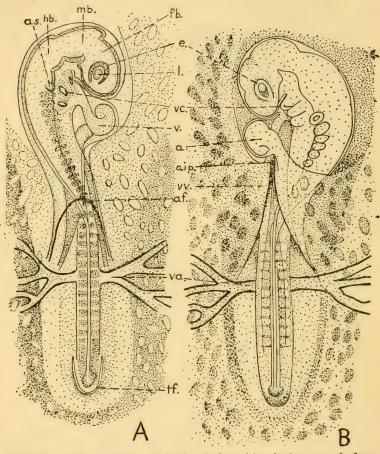
FIG. 98.—Gallus : embryo chick after 60 hours' incubation seen, A, from the dorsal side by transmitted light, B, from the ventral side by reflected light. (After Jenkinson.)

The head-end has turned and is lying on its left side ; the heart is twisting ; the tail-fold has appeared, and the amniotic folds cover half the embryo. *a*, auricular portion of the heart ; *e*, eye ; *l*, lens ; *tf*, tail-fold ; *v*, ventricular portion of the heart ; *vc*, visceral cleft. Other letters as Figs. 91, 93, and 97.

previously covered over the neural tube. The folds join above the embryo, which now finds itself in a sac, the amniotic

cavity, covered over by two membranes of which the inner is the amnion and the outer is the chorion. Both these membranes are of course part of the extra-embryonic ectoderm, and the fact that there are two of them is due to the amniotic fold having two layers as it rises up. At the hind end, the amnion and chorion remain in contact at their point of fusion, forming the so-called sero-amniotic connexion. Extra-embryonic mesoderm gets carried up with the ectoderm in the amniotic fold, and forms a layer on the outer side of the amnion and on the inner side of the chorion. The space between the amnion and the chorion is therefore occupied by extra-embryonic cœlomic cavity. The amniotic cavity is of course lined by ectoderm, and contains fluid. Although laid on dry land, therefore, the chick embryo develops in a fluid medium which may be said to be an artificial " pond," equivalent to the pond in which the (more aquatic) ancestors developed, as the frog now does. The embryo is also protected by the amnion as by a water cushion from shocks and knocks to which the shell may be subjected, and from too sudden changes of temperature.

The Gut.—The base of the amnion grows in beneath the embryo, thus accentuating the folding off of the latter from the rest of the blastoderm. The head-fold has already been noticed, and as the base of the amnion grows in beneath it and backwards, a floor is formed for the most anterior region of the gut. In the same way at the posterior end, a tail-fold develops, and the base of the amnion growing in forms a floor for the hindmost region of the gut. The middle portion of the gut has as yet no floor, and is directly open to the surface of the yolk underneath ; its sides are formed, however, and it is known as the intestinal groove. The passage between the intestinal groove and the foregut, over the edge of the floor of the latter, is called the anterior intestinal portal. Similarly, at the hinder end a posterior intestinal portal is formed. At first the two intestinal portals are far apart, which is the same thing as saying that the formation of the floor of the gut has not yet proceeded very far back from the front end or forwards from the hinder end of the embryo. As development goes

on, however, more and more of the floor of the gut and ventral wall of the embryo is formed, and the intestinal portals come close together leaving only a narrow opening between the cavity of the gut in the embryo and the yolk—the umbilicus.
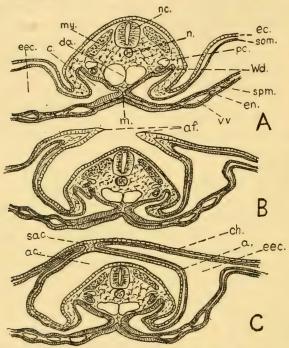
FIG. 99.—Gallus : transverse sections through a chick embryo after three days' incubation through A the hinder, B, the middle, and C, the anterior regions of the trunk ; showing stages in the development of the amnion.

a, amnion ; *ac*, amniotic cavity ; *af*, amniotic fold ; *c*, cœlom ; *ch*, chorion ; *da*, dorsal aorta ; *ec*, ectoderm ; *eec*, extra-embryonic cœlom ; *en*, endoderm ; *m*, dorsal mesentery ; *my*, myotome ; *n*, notochord ; *nc*, nerve-cord ; *pc*, posterior cardinal vein ; *sac*, sero-amniotic connexion ; *som*, somatopleur ; *spm*, splanchnopleur ; *vv*, vitelline vein ; *Wd*, Wolffian duct.

Meanwhile, the extra-embryonic portion of the blastoderm has been extending down over the surface of the yolk, and eventually covers it completely except for a small aperture which is left open, and through which the yolk is separated from the albumen only by the vitelline membrane. The

ectoderm of this region is continuous with and forms part of
the chorion ; the endoderm, continuous with the endoderm
of the embryo, now contains the yolk, and is known as the
yolk-sac.   There is a layer of mesoderm on the inner side of
the ectoderm, and another on the outer side of the yolk-sac,
so that the extra-embryonic cœlomic cavity extends down into
this region.   The yolk-sac contains the store of nourishment
for the developing embryo, and the yolk digested is brought
into the embryo by the blood-vessels of the area vasculosa.
The yolk-sac represents the heap of yolk-cells in the hinder
part of the gut of the developing frog, but there is so much
yolk that it cannot be accommodated inside the cavity of the
gut as in that animal.   Instead, it hangs in a sac beneath the
gut, and gets gradually drawn up as its contents diminish,
until, right at the end of development, it passes up through
the umbilicus into the intestine of the embryo.   Just before
doing so, the albumen surrounding the chorion becomes con-
tained in a sac formed by folds of the latter.   This sac com-
municates with the base of the yolk sac through the aperture
which was left open, and it communicates also with the
amniotic cavity by a reopening of the sero-amniotic connexion.
The amniotic fluid and albumen are therefore able to pass
into the yolk-sac and get absorbed.

Allantois.—Shortly after the formation of the amnion a
median ventral downgrowth is developed from the floor of the
hind gut.   This endodermal sac, covered on the outside by
a layer of mesoderm, is the allantois and it represents the
bladder of the frog.   The allantois grows out into the extra-
embryonic cœlomic cavity, and its size increases as that of
the yolk-sac diminishes.   It soon occupies almost the entire
space within the chorion which is not filled by amnion and
yolk-sac.   Its outer wall becomes applied to the inner surface
of the chorion, and the extra-embryonic cœlomic cavity between
them disappears by the fusion of the two layers of mesoderm
(on the inner side of the chorion and on the outer side of the
allantois).   This fused layer of allantois and chorion now
lies close against the inner surface of the shell, only separated
from it by the shell-membranes ; it is also highly vascular

being supplied by blood-vessels which run out from the embryo along the allantoic stalk. As the shell is porous, the blood-vessels of the allantois form a region where oxygen is taken
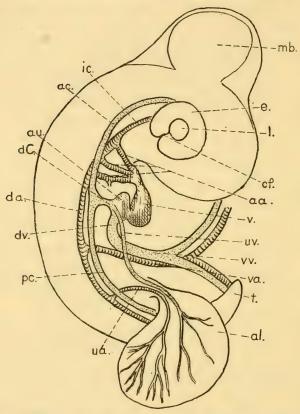
FIG. 100.—Gallus : view of an embryo chick after four days' incubation, from the right side.

aa, arterial arches ; *ac*, anterior cardinal ; *al*, allantois ; *au*, auricular portion of the heart ; *cf*, choroid fissure of the optic cup ; *da*, dorsal aorta ; *dC*, ductus Cuvieri ; *dv*, ductus venosus ; *e*, optic cup ; *ic*, internal carotid artery ; *l*, lens ; *mb*, midbrain ; *pc*, posterior cardinal ; *t*, tail ; *ua*, umbilical artery ; *uv*, umbilical vein ; *v*, ventricular portion of the heart ; *va*, vitelline artery ; *vv*, vitelline vein.

into and carbon dioxide is given off from the blood. The allantois therefore functions as a respiratory organ, and is of the highest importance. The gill-slits do not function as

respiratory organs, for they communicate with the amniotic cavity in which the oxygen cannot be renewed.
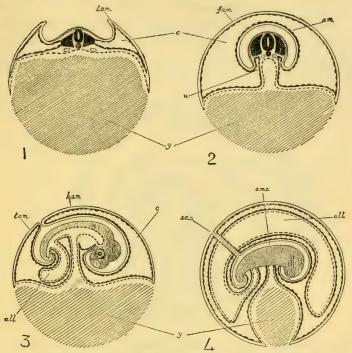
FIG. 101.—Diagrams showing the formation and relations of the amnion, chorion, yolk-sac and allantois in the chick. (From Jenkinson.)

1, transverse section ; the amniotic folds are rising up, but the gut is not yet folded off from the yolk. 2, transverse section ; the amniotic folds have met and fused ; the amniotic cavity is closed and the amnion is separated off from the chorion ; the gut is beginning to be folded up from the yolk. 3, longitudinal section ; the amniotic folds are about to fuse ; the allantois is growing out from the hind gut of the embryo. 4, longitudinal section ; the amniotic cavity is closed and the amnion is separated off from the chorion except at the sero-amniotic connexion ; the yolk is now almost enclosed in a yolk-sac which remains open beneath ; the allantois is greatly enlarged. *all*, allantois ; *am*, amnion ; *amc*, amniotic cavity ; *c*, cœlom ; *fam*, chorion ; *ham*, head-fold of the amnion ; *lam*, lateral amniotic fold ; *sac*, sero-amniotic connexion ; *tam*, tail-fold of the amnion ; *u*, side wall of the gut ; *y*, yolk.

Another function of the allantois is excretion, for the Wolffian ducts run into the hind gut (cloaca) near its base, and it acts as a reservoir for the excretory products accumulated

during the embryonic life. At the end of this period the allantois is not drawn up into the embryo, but nipped off at the umbilicus and left behind.

The relations of the embryonic membranes are simple to make out if it is remembered that mesoderm underlies ectoderm, and mesoderm overlies endoderm. All the boundaries of any particular cavity are continuous when traced
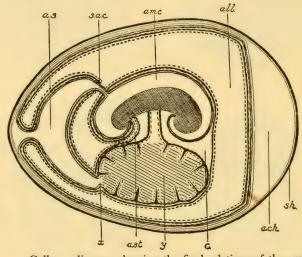
FIG. 102.—Gallus : diagram showing the final relations of the embryonic membranes. (From Jenkinson, after Duval and Lillie.)

ach, air-chamber ; *all*, allantois the outer wall of which is closely pressed against the shell-membrane ; *amc*, amniotic cavity which communicates with the (*as*) albumen sac through the reopened (*sac*) sero-amniotic connexion ; *ast*, allantoic stalk ; *c*, extra-embryonic cœlom ; *sh*, shell ; *y*, yolk in the yolk-sac which still communicates with the albumen-sac ; *x*, point at which the yolk-sac will eventually close.

right round, and are formed from one germ-layer. They are consistent in their arrangement, so that an endodermal cavity (gut, yolk-sac or allantois) cannot communicate with a cavity lined by mesoderm (cœlom), or with one lined by ectoderm (amnion, or atrium of Amphioxus).

Vascular System.—At an early stage, the blood-islands of the area vasculosa become connected up with a pair of anterior vitelline veins which run towards the embryo from each side,

and pass just in front of the anterior intestinal portal where they fuse in the middle line. This vessel, lying immediately beneath the floor of the fore gut, represents the subintestinal vein of the frog, and in this region it becomes differentiated into the heart. It is suspended from the floor of the fore gut by a mesentery, the dorsal mesocardium, and that part of the cœlomic cavity into which it hangs will become the pericardium. At early stages, the heart is still outside the embryo, and it is not drawn into it until the base of the amnion has grown in
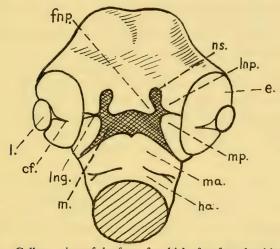
FIG. 103.—Gallus : view of the face of a chick after four days' incubation.

cf, choroid fissure of the optic cup ; e, optic cup ; fnp, fronto-nasal process ; ha, hyoid arch ; l, lens ; lng, lachrymo-nasal groove ; lnp, lateral nasal process ; m, mouth ; ma, mandibular arch ; mp, maxillary process ; ns, nasal sac.

beneath it. The anterior vitelline veins from the yolk-sac soon become replaced by the larger pair of posterior vitelline veins.

Running forwards from the heart, the aortic arches run up round the fore gut (pharynx) on each side passing between the gill-slits in the visceral arches. The hyomandibular and three pairs of branchial pouches are developed as outgrowths from the endoderm to the ectoderm. Of these, the hyomandibular and the first two branchials actually become perforated for a

time, and place the cavity of the fore gut in communication with that of the amnion.

In the embryo, paired dorsal aortæ develop, beneath the notochord. Anteriorly they connect with the aortic arches, and posteriorly at an early stage they simply spread out over the yolk-sac on each side forming the vitelline arteries. Later, the single median dorsal aorta arises by the fusion of the paired vessels (as far forwards as the pharynx), and it extends back behind the vitelline arteries into the tail as the latter is formed.

The aortic arch in the 4th visceral arch becomes the systemic (that on the left disappears), that in the 6th arch the pulmonary. The pulmonary arches also connect with the dorsal aorta by the ductus arteriosus.

The cardinal veins also arise as paired vessels, on each side of the aorta, and they communicate with the heart across a transverse septum by means of the ductus Cuvieri. Beneath the hind portion of the posterior cardinal veins, the subcardinal veins arise, in the region of the mesonephros. The subcardinal veins acquire connexion with the developing inferior vena cava.

As the anterior intestinal portal moves farther back in the embryo, the fusion of the two posterior vitelline, or omphalemesenteric veins, with one another becomes more extensive. This combined vessel, which lies in the region of the developing liver and behind the heart, is known as the ductus venosus. At the hind end of the ductus venosus, the two posterior vitelline veins are separate, but farther back still they fuse together again twice : in one place dorsal to the gut, and in another place behind again, ventral to the gut. The piece on the left side between the dorsal point of fusion and the ductus venosus disappears ; the piece on the right side between the dorsal fusion and the ventral fusion behind it disappears also. The net result of all these modifications is that the vitelline veins run into the embryo on each side from the yolk-sac and join beneath the gut. From this point a single vein runs forwards and makes one complete twist round the gut in the direction of the thread of a corkscrew, and runs into the ductus venosus. Part of these posterior vitelline veins becomes

the hepatic portal vein, and the ductus venosus becomes the hepatic veins and the base of the inferior vena cava.

The allantois is supplied with blood by the umbilical arteries (branches from the artery to the hind leg), and drained by the umbilical veins. These run in the side wall of the abdominal cavity and correspond to the lateral abdominal veins of the dogfish. At first they run into the ductus Cuvieri of their side, but later the right umbilical vein is reduced and
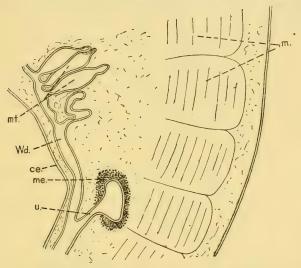
Fig. 104.—Longitudinal section through an embryo showing the development of the metanephros.

(Actually, this section is of a mammal, not a bird, but the difference is immaterial.) The ureter arises as an outgrowth from the Wolffian duct. ce, cœlomic epithelium ; m, myotomes ; me, metanephrogenous tissue ; mt, mesonephric tubules ; u, ureter ; Wd, Wolffian duct.

the left one runs into the ductus venosus. At all events, the blood from the allantois, where it has been oxygenated, runs into the right auricle of the heart when the latter becomes subdivided by interauricular and interventricular septa. The left auricle receives the pulmonary veins. The lungs are, however, not functional, and by the breaking down of the septum between the auricles, part of the blood from the allantois is able to get from the right to the left auricle, and so to the left

ventricle and the systemic arch without going through the right ventricle. The remainder of the blood passes through the right ventricle to the pulmonary arches, and from them through the ductus arteriosus to the dorsal aorta. Little if any goes to the lungs. The interauricular septum is reconstituted after hatching, when the lungs are open and functional, and oxygenated blood reaches the left auricle from the lungs. The interventricular septum is complete.

Kidneys.—With the exception of the urino-genital organs, the remaining organs of the chick develop in a manner very similar to that which obtains in the frog, and no useful purpose would be served by going over them in detail. The limbs may be mentioned, since they show in their development certain characters which are more primitive than the definitive adult condition; and especially the urino-genital system is worthy of note. Not only does it differ in some respects radically from that of the frog, but in others it shows certain features more clearly.

In some half a dozen segments in the anterior region of the trunk, the intermediate cell-mass or nephrotome of each segment pushes out a rod of cells which curves backwards and meets and fuses with the similarly produced rod from the segment next behind it. Each of these rods represents a tubule of the pronephros; they are solid instead of being hollow and opening into the cœlom by ciliated funnels, because the pronephros is degenerate in the chick, and does not even function as an excretory organ. However, the rod of cells formed by the pronephros on each side in this way grows back to the cloaca, and later becoming hollow, forms the pronephric duct.

In about a dozen segments, behind the pronephros, the mesonephric tubules develop. Like the pronephros, they are segmental in origin, and as they grow out from the intermediate cell-mass, they find the pronephric duct so to speak ready-made for them. They connect with it which now becomes known as the mesonephric or Wolffian duct. The mesonephric tubules do not as a rule open into the splanchnocœlic cavity; they have no cœlomic funnels. The tubules give rise by

branching to a number of Bowman's capsules, and each becoming vascularised by a glomerulus becomes a Malpighian corpuscle. The mesonephros is the functional kidney of the embryo, and is therefore present in the early life of both sexes. Later, it is preserved only in the male, for it establishes connexion with the testis by means of the vasa efferentia, and the Wolffian duct functions as the vas deferens. It disappears in the female.

The kidney of the adult is the metanephros. It is formed after the mesonephros, and at a time when the segmental
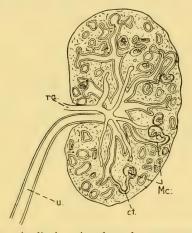
FIG. 105.—Longitudinal section through a metanephric kidney.

Showing the Malpighian corpuscles (*Mc*) in communication with the ureter (*u*) by means of the collecting tubules (*ct*) ; *ra*, renal artery.

arrangement of the intermediate cell-mass has been lost. A diverticulum develops from the base of the Wolffian duct, near the cloaca ; this is the ureter. The ureter grows forwards dorsal to the mesonephros, and branches repeatedly forming a large number of collecting tubules. The metanephric tubules, or Bowman's capsules, arise from an indistinct heap of cells of the intermediate cell-masses belonging to one or two segments of the hinder region of the body, and called simply the metanephrogenous tissue. These capsules hollow out and connect with the collecting tubules which were formed by the

branching of the ureter. Each capsule is vascularised by a glomerulus, and forms a Malpighian corpuscle. The metanephric tubules never have cœlomic funnels.

So long as the mesonephros functions as an excretory organ, there is a renal portal system formed by the hinder region of the posterior cardinal veins. These veins filter through the mesonephros, and are collected into the so-called subcardinal veins, which contribute to the formation of the inferior vena cava. The renal portal system disappears with the excretory function of the mesonephros ; meanwhile the metanephros has developed and renal veins connect its glomeruli to the inferior vena cava. The posterior cardinals then run into these renal veins.

The Müllerian ducts develop in both sexes as grooves in the cœlomic epithelium which become closed over to form tubes, and these tubes grow back to the cloaca. In the male, both these ducts disappear ; in the female the right duct is lost and that on the left side persists as the definitive oviduct.

Limbs.—The limbs appear as buds at a stage relatively earlier than that at which they arise in the frog. Their interest lies in the fact that the cartilaginous skeleton of the limbs in larvæ reflects the primitive condition, before the modifications of the wings and the mesotarsal joints arose. In the wrist, the distal carpals and the metacarpals are at first separate ; there is as yet no carpo-metacarpus. There are also vestiges of the 1st and 5th digits, so that the wing at this stage resembles a more normal pentadactyl fore limb. Similarly in the hind limb, the proximal tarsal cartilages are not yet fused on to the tibia to form a tibio-tarsus, neither are the distal tarsals yet joined on to the metatarsals to give rise to a tarso-metatarsus.

The early stages of the pelvic girdle are of great interest, for the pubis when it first arises in cartilage points forwards and downwards ; it is only later that it extends back beneath the ischium.

Hatching.—Meanwhile the mouth and the anus have broken through into the gut as the result of the sinking in of the stomodæum and proctodæum. As the chick grows during its development, its position changes to accommodate it to the

surrounding membranes. At an early stage it turns and lies on its left side, and later, its body lies along the long axis of the egg with its head near the blunt end of the shell, which is where the air-chamber is situated. Its beak pierces the inner shell-
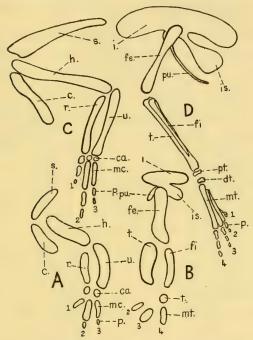
FIG. 106.—Gallus : views of the (cartilaginous) skeleton of the limbs and girdles of embryo chicks, A and B, after 5 days' C and D after 9 days' incubation, as seen from the left side.

A and C, pectoral girdle and limb ; B and D, pelvic girdle and limb. Note that in the earlier stage the pubis points forwards. *c*, coracoid ; *ca*, carpals ; *dt*, distal tarsals (which will fuse with the metatarsals to form the tarso-metatarsus) ; *fe*, femur ; *fi*, fibula ; *h*, humerus ; *i*, ilium ; *is*, ischium ; *mc*, metacarpal ; *mt*, metatarsal ; *p*, phalanx ; *pt*, proximal tarsals (which will fuse with the tibia to form the tibio-tarsus) ; *pu*, pubis ; *r*, radius ; *s*, scapula ; *t*, tibia ; *u*, ulna.

membrane, and it begins to breathe the air in the air-chamber into its lungs, often making the characteristic " peep peep " sound. The connexions between the pulmonary arteries and the dorsal aorta (ductus arteriosus) disappear, and more and more blood passes through the lungs. The yolk-sac has

been completely absorbed within the body. The beak of the upper jaw bears a sharp projection, the egg-tooth, with which the chick pierces the shell, and soon after, it emerges, having severed its connexion with the allantois. The septum between the auricles of the heart is reformed, and the chick now lives in the same manner as the adult bird.

Feathers.—Feathers begin developing at about the seventh day of incubation and the first sign of their appearance is in the form of a thickening of the epidermis overlying a condensation of the dermis, and forming a papilla. The rudiment of the feather soon becomes conical and eventually takes the form of an elongated cylinder. The papilla at its base becomes sunk beneath the general level of the skin forming a follicle. The deepest layer of the epidermis differentiates into a number of longitudinal thickened ridges, two of which will become the rachis, and the remainder will give rise to the barbs which come off from the rachis. At this stage they are still rolled up inside the cylinder and covered by the outer layer of epidermis forming the feather-sheath. The central dermis is nutritive in function, and eventually degenerates. The vane of the feather is formed by the shedding of the sheath, the splitting of the cylinder on the side opposite the rachis, and the flattening out of the barbs which have thus been released, on each side of the rachis. The former cylindrical nature of the feather is betrayed by the presence of a hole at the base of the quill—the inferior umbilicus—and another at the bottom of the vane (between it and the aftershaft), the superior umbilicus. The aftershaft represents the thickenings of deeper layers of the epidermis on the side of the cylinder opposite the rachis, and below the lowermost barbs belonging to the rachis.

The feathers of the adult bird, pennæ, plumulæ, and filoplumes, are typically preceded by " nestling-down " in the form of prepennæ, preplumulæ, and prefiloplumes respectively. There are two generations of prepennæ, but in the majority of birds it is the first generation which forms the nestling-down, and the second is reduced. Both generations are present in the penguins.

The nestling-down feathers are carried out on the tip of
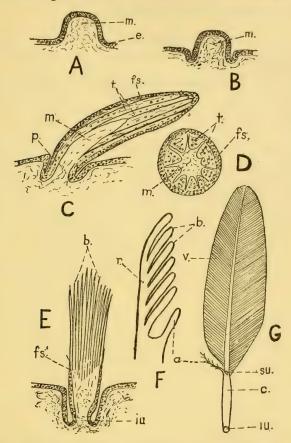
FIG. 107.—Sections and diagrams showing the development of feathers.

A, section through an early papilla; B, slightly later stage in which the sides of the papilla are beginning to sink beneath the surface; C, longitudinal section through a young feather in which the epidermal thickenings are present, but the feather-sheath has not yet disappeared; D, transverse section of C; E, the feather-sheath has been shed from the end of the feather and the barbs are freed; F, diagram showing the relations of the rachis, barbs, and aftershaft; G, view of an adult feather. *a*, aftershaft; *b*, barbs; *c*, calamus; *e*, ectoderm; *fs*, feather-sheath; *iu*, inferior umbilicus; *m*, mesoderm; *p*, papilla; *r*, rachis; *su*, superior umbilicus; *t*, ectodermal thickenings (which will give rise to the barbs); *v*, vane.

the adult feathers, for the latter grow from the same papillæ

Q

as their predecessors, and when the adult feathers are properly formed, the nestling-down is worn off.

LITERATURE

JENKINSON, J. W. Vertebrate Embryology. Oxford, at the Clarendon Press, 1913.

KELLICOTT, W. E. Chordate Development. Henry Holt, New York, 1913.

LILLIE, F. R. The Development of the Chick. Henry Holt, New York, 1919.

CHAPTER XIV

DEVELOPMENT OF LEPUS (THE RABBIT)

Fertilisation.—The egg is very small, and contains very little yolk. It is surrounded by a vitelline membrane secreted by itself, and by a secondary membrane formed from the follicle-cells, the zona pellucida. The follicle-cells are several layers thick surrounding each egg-cell, which however they do not fit closely. There is a large space inside the follicle filled with fluid and bathing the egg, which gives the characteristic appearance of the Graafian follicle, typical of mammals. One polar body is extruded in the ovary, the second is extruded after fertilisation.

Ovulation is the process of escape of the egg from the ovary. The follicle vacated by the egg becomes filled by the great increase in size of the follicular cells and by the ingrowth of connective tissue and blood-vessels, and becomes a corpus luteum. Should the egg just ovulated be fertilised, the corpus luteum becomes an important structure, functioning as a gland of internal secretion, and among its functions are the following. It prevents ovulation of other eggs during the period of pregnancy, it stimulates the uterus to hypertrophy and so prepares for the reception and fixation of the embryo, and it stimulates the mammary glands to secrete. The corpus luteum disappears at the end of the period of gestation, but if no pregnancy has ensued it disappears soon after ovulation.

Many mammals ovulate spontaneously during periods of "heat," or œstrus, and the mouse is among them. Others, such as the rabbit, only ovulate after copulation. During copulation sperms are introduced into the vagina, and they make their way up through the uteri to the oviducts, near the top of which

they meet and fertilise the egg. Fertilisation is therefore internal, as in the chick.

Cleavage.—Cleavage is total and gives rise to a ball of cells, or morula. A cavity appears within it, and it soon becomes differentiated into an outer layer and an inner mass of cells.
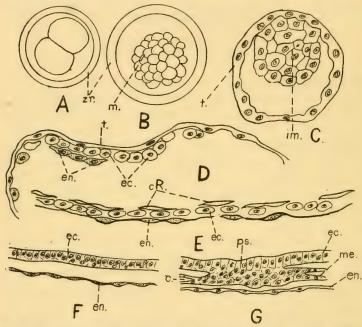
FIG. 108.—Lepus : early stages in the development of the rabbit. (After Assheton.)

A, two-cell stage, enclosed by the zona pellucida (*zr*) ; B, morula (*m*) stage ; C, blastocyst showing the differentiation into the trophoblast (*t*) and the inner mass (*im*) ; D, the inner mass has become the embryonic plate and is differentiated into ectoderm (*ec*) and endoderm (*en*) ; E, the trophoblast overlying the embryonic plate—the cells of Rauber (*cR*)—disappear ; F, after the disappearance of the trophoblast over the embryonic plate ; G, transverse section through the primitive streak (*ps*). *c*, cœlom ; *me*, mesoderm.

The former is called the trophoblast, and the whole structure is known as a blastocyst.

Implantation.—The lining of the uterus has on its meso-metrial side (see p. 276) a pair of prominent folds, which project into the cavity or lumen of the uterus. To these, the

blastocyst becomes attached by means of its trophoblast. This process is called implantation.

Formation of the Embryo.—The blastocyst enlarges and expands in the cavity of the uterus. The cells of the inner mass become arranged in the form of a flattened disc, immediately beneath the trophoblast. This disc is known as the embryonic plate. At the same time, the inner mass gives rise to a layer of cells which grow as an epithelium lining the
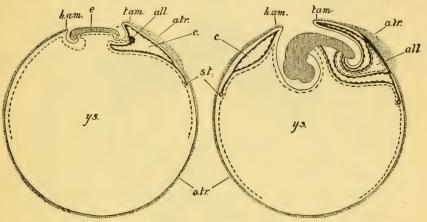
FIG. 109.—Diagrams showing the formation of the amnion in the rabbit. (From Jenkinson, after van Beneden.)

The earlier stage is on the left ; the later stage on the right. Since the cells of Rauber have disappeared, the embryo is at the surface of the blastocyst until the amnion has formed. *all*, allantois ; *atr*, region of the trophoblast where the allantoic placenta will be formed ; *c*, extra-embryonic cœlom ; *e*, embryo ; *ham*, head amniotic fold ; *otr*, region of the trophoblast where the omphaloidean placenta is formed ; *st*, sinus terminalis (blood-vessel) of the area vasculosa ; *tam*, tail amniotic fold. *ys*, yolk-sac.

inner surface of the trophoblast. This layer is endoderm (also called the " lower layer "), and the cavity which it encloses represents the yolk-sac of the chick. Here, however, there is no yolk, and the yolk-sac is consequently empty.

The cells of the trophoblast immediately overlying the embryonic plate (the cells of Rauber) disappear, and the embryonic plate thus comes to the surface of the trophoblast. A primitive streak is formed in the centre of the embryonic plate, and, as in the chick, it proliferates mesodermal cells

to each side, and forms the notochord in the middle line as it retreats towards the hind end of the embryo. Neural folds rise up and enclose the neural tube, and the embryo becomes
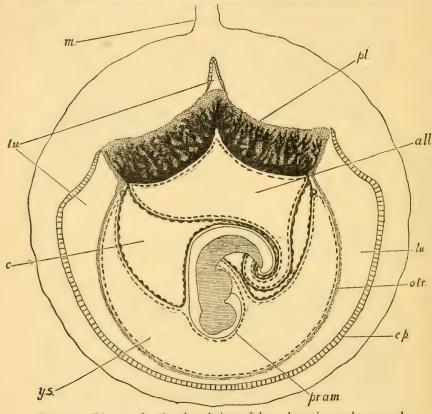
FIG. 110.—Diagram showing the relations of the embryonic membranes and placenta of the rabbit, as seen in an idealised transverse section of the uterus. (From Jenkinson, after Duval and van Beneden.)

all, allantois ; *c*, extra-embryonic cœlom ; *ep*, epithelium of the uterus ; *lu*, cavity of the uterus ; *m*, mesometrium ; *otr*, omphaloidean trophoblast ; *pl*, placenta (allantoic) ; *pr am*, proamnion ; *ys*, yolk-sac.

folded up from the surrounding tissue by the head-fold and tail-fold. In this way, the gut begins to be formed, and, as in the chick, anterior and posterior intestinal portals arise (see p. 211).

The amnion arises by the upgrowth of folds at the edge of the embryonic plate. The hinder amniotic fold develops faster than that in front, and when these folds meet, the embryo is no longer at the surface of the trophoblast, but folded away within it. The embryo is then enclosed in the amniotic cavity, just as in the chick, and the trophoblast of the rabbit corresponds to the chorion of the chick, the relations of which are identical (see p. 211). (It may be mentioned that in some other mammals such as the mouse, the amnion is not formed quite in this way, but arises precociously, even before the embryo (see p. 254). The rabbit has been chosen for description here because its development is so easily comparable with that of the chick.)

The mesoderm splits into somatic and splanchnic layers with the cœlomic cavity between them. The splanchnic layer overlies the yolk-sac. The somatic layer grows up round the amnion and separates the latter from the trophoblast.

An area vasculosa develops in the wall of the yolk-sac, and the blood-vessels so formed extend as far as the sinus terminalis. The lower wall of the yolk-sac is not vascularised. In some mammals this lower wall of the yolk-sac with its overlying trophoblast persist for some time, and absorb nourishment from the walls of the uterus. In the rabbit, however, this " omphaloidean " region of the trophoblast together with the lower wall of the yolk-sac disappear, and the cavity of the yolk-sac is then openly continuous with that of the lumen of the uterus. This disappearing part of the blastocyst contained neither blood-vessels nor mesoderm.

Placenta.—Meanwhile, the upper part of the trophoblast which is in contact with the wall of the uterus on the mesometric side becomes much thicker, forming a syncytium (or plasmoditrophoblast). The more basal part of the trophoblast, between the syncytium and the mesoderm, retains its cell-boundaries (and is called the cyto-trophoblast). The allantois grows out from the region of the hind gut and brings with it a covering layer of mesoderm and blood-vessels. The mesoderm covering the allantois fuses with the mesoderm underlying the cyto-trophoblast, and the allantoic blood-vessels make

their way into the trophoblast. In this way the placenta is formed, and since it is related to the allantois, it is called an " allantoic placenta." The placenta is an organ which places the mother and embryo in physiological communication, for the interchange of substances. The epithelium of the wall of the uterus disappears where the trophoblast touches it, with the result that the trophoblast is in contact with the subepithelial tissues and blood-vessels of the uterine wall. The blood from these maternal vessels bathes the surface of the trophoblast.
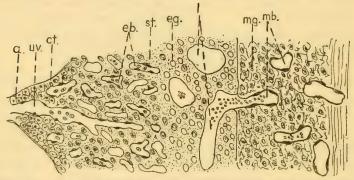
FIG. 111.—Section through a part of the allantoic placenta of the rabbit.

The maternal tissue is on the right, the embryonic tissue on the left. They can often be distinguished by the fact that the red blood-corpuscles of the embryonic blood have not yet lost their nucleus. *a*, allantois ; *ct*, cyto-trophoblast ; *eb*, embryonic blood-vessels ; *eg*, embryonic glycogenic layer ; *l*, lacunæ in the trophoblast and filled with maternal blood ; *mb*, maternal blood-vessels ; *mg*, maternal glycogenic layer ; *st*, syncytium or plasmodi-trophoblast ; *uv*, umbilical vein.

Further, the trophoblast, which in this region is now thick, becomes hollowed out by a number of spaces or lacunæ ; and these lacunæ become filled by maternal blood which oozes out from the wall of the uterus.

The capillaries of the allantois branch in the substance of the placenta, and the blood which they contain is separated from the maternal blood only by the lining of the capillaries and the surface of the trophoblast. (The blood of mother and embryo are never in direct communication.) Across these, substances are passed by diffusion. The maternal blood supplies not only oxygen but food, and the embryonic blood

brings carbon dioxide and excretory products which are passed on into the maternal circulation. The placenta therefore functions as a respiratory, nutritive, and excretory organ. At the same time, a certain amount of nutriment is obtained from the glands of the uterus, and is either ingested phagocytically by the trophoblast or absorbed into the blood-vessels of the yolk-sac (the cavity of which opens freely into that of the uterus). But the functions of the placenta do not end there, for it also serves as a store of food material for the developing embryo. In particular, glycogen is accumulated in the placenta at early stages before the embryo has a liver of its own ; when the latter develops, the gycogen content of the placenta decreases.

The vascular system of the embryo rabbit resembles that of the chick, but the posterior cardinals persist as the azygos and hemiazygos veins. The blood from the placenta arrives in the umbilical veins, of which the right disappears and the left runs into the ductus venosus and so to the right auricle. As in the chick, the septum between the auricles in the heart is perforated, and the oxygenated blood from the placenta can get through to the left auricle, left ventricle, and so to the carotids and brain, which requires the purest blood in the body. The pulmonary artery connects with the aorta on the left side by the ductus arteriosus, so that the remainder of the venous blood in the right auricle passes through the right ventricle, pulmonary artery, and ductus arteriosus to the aorta below the place where the carotids come off, and does not have to go through the lungs. The ductus arteriosus degenerates and the perforation of the interauricular septum is closed at birth when the lungs begin to function. The right systemic arch disappears.

As in lower forms, the fore gut and the hind gut remain blind for a long time. In these regions the endoderm becomes apposed to the overlying ectoderm forming the oral plate and cloacal plate respectively. Perforation of these give rise to the mouth and cloaca, which latter is divided into anus and urino-genital aperture. The bladder forms from the base of the allantois.

The urino-genital ducts develop much as in the chick, except that the right oviduct persists, and the testis descends into the scrotum.

From the fact that the perforation of the mouth does not occur at the extreme front end, but in the centre of the oral membrane, a small pocket is formed morphologically in front of the mouth. This is the so-called preoral gut. In a similar way, a post-anal gut is left after perforation of the anus.

In the region of the pharynx, the gill-pouches arise as outpushings from the gut to the ectoderm. They do not, however, become perforated.

Several structures enter into the formation of the diaphragm. The transverse septum moves backwards a considerable distance during development, and it is followed in its course by the phrenic nerve. The transverse septum forms the ventral portion of the diaphragm, and the wall which separates the pericardium from that part of the perivisceral cavity into which the lungs extend. The dorsal portion of the diaphragm separates this pleural cœlom from the abdominal cavity behind, and it is formed by the growth of the mesenteries associated with the liver (which enlarges), kidneys, lungs, and gut.

As the placenta and the embryo increase in size, the uterus becomes enlarged to accommodate them. This is effected by a great increase in the size of the smooth muscle-cells of which the wall of the uterus is composed, without any increase in their number.

When the period of gestation is accomplished, the amnion breaks and the embryo is expelled by the contractions of the muscular walls of the uterus. The umbilical cord is torn. The placenta also becomes detached from the wall of the uterus, and, together with clots of blood and debris, is expelled as the after-birth.

Hair.—The development of hair starts by a thickening of the deeper layer of the epidermis, and its downgrowth into the dermis forming a little cylinder. At its base a papilla is formed, and just above this, the epidermal cells proliferate and give rise to the shaft of the hair. This elongates as more material is added to it from beneath, and it finally emerges

from the follicle and grows freely out. The centre of the hairshaft is composed of the medulla ; surrounding this is the cortex, and round this again is the cuticle. The outer wall of the follicle forms a sheath round the base of the hair, and the following layers can be made out in it. In contact with the cuticle of the hair is the cuticle of the sheath, and next outside that are Huxley's layer, Henle's layer, and the main
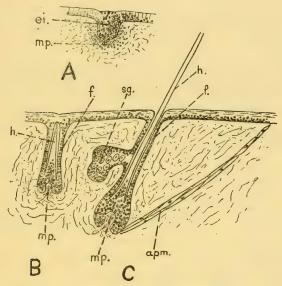
FIG. 112.—Sections through the skin of mammalian embryos showing stages in the development of the hairs.

A, early stage showing the ectodermal inpushing (*ei*) and the concentration of the mesoderm to form a papilla (*mp*) ; B, the ectoderm forms a follicle (*f*) inside which the hair (*h*) is developing ; C, late stage after the hair has erupted from the surface. *apm*, arrector pili muscle ; *sg*, sebaceous gland.

epidermal layer of the sheath. Surrounding this again is the dermal sheath of the follicle. The epidermis of the wall of the follicle gives rise to little pouches which become the sebaceous glands. Some mesenchyme cells outside the follicle become differentiated into smooth muscle-fibres ; they gain attachment to the wall of the follicle and become the arrector muscles of the hair.

LITERATURE

BONNET, R. Lehrbuch der Entwicklungsgeschichte. Parey, Berlin, 1920.

JENKINSON, J. W. Vertebrate Embryology. Oxford, at the Clarendon Press, 1913.

KELLICOTT, W. E. Chordate Development. Henry Holt, New York, 1913.

PRENTISS, C. W., and, AREY, L. B. A Laboratory Manual and Text-book of Embryology. Saunders Co., Philadelphia and London, 1922.

COMPARATIVE ZOOLOGY OF CHORDATES

(*Most of the extinct groups have been omitted.*)

Phylum.	**Chordata.**	Animals with gill-slits, notochord, dorsal tubular nerve-cord, and post-anal tail.
Subphylum.	**Hemichordata.**	Very lowly forms with a small notochord only in the anterior region of the body, *e.g.* Balanoglossus.
Subphylum.	**Protochordata.**	Without a specialised head or skull.
Class.	**Urochordata.**	Degenerate forms with a notochord only in the tail of the larva, *e.g.* Ascidia.
Class.	**Cephalochordata.**	Primitive forms with the notochord extending the whole length of the body, *e.g. Amphioxus.*
Subphylum.	**Craniata.**	With a specialised head and skull, paired eyes, ears, and noses, heart and cœlomostomic kidneys.
Grade.	**Anamnia.**	Without an amnion. Breathing by gills at some stage of life if not altogether.
Branch and Class.	**Cyclostomata.**	With a round sucking mouth, no jaws or paired fins, *e.g. Petromyzon* (lamprey) Myxine (hag).
Branch.	**Gnathostomata.**	With biting jaws, stomach, paired fins or limbs, Wolffian and Müllerian ducts.

Class.	**Pisces (Fish).** With paired fins.
Grade.	**Chondrichthyes.** With cartilaginous skeleton only.
Order.	**Selachii.** Gills u n c o v e r e d, hyostylic or amphistylic, *e.g.* *Scyllium*, sharks and rays.
Order.	**Holocephali.** Pseud-autostylic, *e.g.* Chimæra.
Grade.	**Osteichthyes.** With bony skeleton, lung or air-bladder.
Subclass.	**Teleostomi.** With air-bladder, hyostylic, *e.g.* *Gadus* (cod).
Subclass.	**Dipnoi.** Lung used for breathing, *e.g.* *Ceratodus*.
Class.	**Amphibia.** With an aquatic gill-breathing larval stage followed by a terrestrial air-breathing adult.
Order.	**Labyrinthodontia** (**or Stegocephalia**). Primitive extinct forms with a complete roofing to the skull, *e.g.* Eogyrinus.
Order.	**Urodela.** With a tail in the adult, *e.g.* *Triton* (newt).
Order.	**Anura.** Without a tail in the adult, *e.g.* *Rana* (frog).
Order.	**Gymnophiona.** Limbless, *e.g.* Ichthyophis.
Grade.	**Amniota.** Embryo develops on land inside an amnion.
Class.	**Reptilia.** Body covered with horny scales, cold-blooded.
Subdivision.	**Sauropsida.** Reptiles related to the birds.
Order.	**Chelonia.** Body enclosed in a carapace, *e.g.* Testudo (tortoises and turtles).
Order.	**Rhynchocephalia.** Primitive forms, *e.g.* Sphenodon.
Order.	**Iacertilia.** Quadrate loose, *e.g.* *Lacerta* (lizard).
Order.	**Ophidia.** Both halves of lower jaw loose, *e.g.* Vipera (snakes).
Order.	**Crocodilia.** Heart 4-chambered, *e.g.* Crocodilus.
Subdivision.	**Theropsida.** Reptiles related to the mammals.
Class.	**Aves (Birds).** With feathers, warm-blooded.
Subclass.	**Palæognathæ.** With a large pre-vomer, *e.g.* Struthio (Ostrich).

Subclass.	**Neognathæ.** With a small prevomer, *e.g. Columba* (pigeon), *Gallus* (fowl).
Class.	**Mammalia.** Mammary glands, hair, diaphragm, warm-blooded.
Grade and Subclass.	**Monotremata.** With a cloaca, *e.g.* Ornithorhynchus (duck-billed-platypus).
Grade.	**Ditremata.** Anus and urinogenital apertures separate.
Subclass.	**Marsupialia.** With marsupial pouch, *e.g.* Perameles.
Subclass.	**Placentalia.** Well-formed allantoic placenta, *e.g. Lepus* (rabbit).

NOTE.—**Vertebrata** may be used as roughly synonymous with **Craniata. Tetrapoda** includes **Amphibia** and **Amniota.**

CHAPTER XV

THE BLASTOPORE

THE blastopore is one of the most important structures in development, for as a result of the processes which are entailed in its formation the fundamental architecture of the future embryo is laid down. Further, experimental investigations have shown that the region of the dorsal lip of the blastopore (which is the first part of the blastopore to develop) is responsible for organising the embryo. That is to say that it determines the place of formation of the various organs, and is necessary for the start of the processes of differentiation. The blastopore itself introduces the first differentiation (after the establishment of the axis of the egg in the ovary, and of the plane of bilateral symmetry by the point of entrance of the sperm) in that it converts the single-layered hollow ball (blastula) into the double-layered bowl (gastrula). In those animals where the relation of the sperm's entrance point to the blastopore is known (amphibia), it is found that the dorsal lip of the blastopore arises opposite the sperm-entrance point, and marks the dorsal side of the future embryo.

In the development of the dogfish, the egg contains so much yolk that cleavage is incomplete or meroblastic, and a disc of cells or blastoderm is formed lying on the top of the yolk. Now the important point to notice is that all round the edge of this blastoderm, cells are growing over the yolk and tucking-in underneath the upper layer of the blastoderm to form endoderm. In fact, the edge of the blastoderm is the rim of the blastopore, and mesoderm-cells are also proliferated from it. The embryo forms in front of the posterior edge of the blastoderm, which is the dorsal lip of the blastopore, and does not

wait for the blastopore to close. Indeed, this takes a long time, for the anterior edge of the blastoderm has to grow a long way down and back under the yolk before it comes up underneath and opposite the dorsal lip to form the ventral lip of the blastopore.

The edge of the blastoderm in the dogfish corresponds to
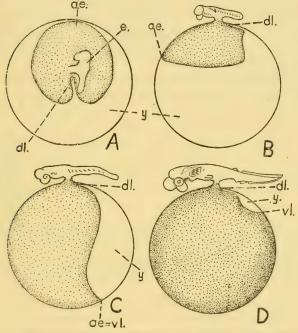
FIG. 113.—Views of a developing embryo of a dogfish. (After Jenkinson.) A from above ; B, C, and D from the left side. The lips of the blasto-pore are formed from the edge of the blastoderm. *ae*, anterior edge of the blastoderm ; *dl*, dorsal lip of the blastopore ; *e*, embryo ; *vl*, ventral lip of the blastopore ; *y*, yolk.

the edge of the pigmented cells of the animal hemisphere in the frog, and this is the place where the overgrowing lip which is the rim of the blastopore arises in the frog also. All round the rim of the blastopore, the ectoderm, mesoderm, and endoderm are in contact. In the case of the frog, the blasto-pore starts a little below the equator of the spherical embryo,

and as it grows down to latitudes nearer the vegetative pole, the diameter of the blastopore naturally decreases. Any given point on the rim of the blastopore grows straight down along a meridional line towards the vegetative pole ; but as the diameter of the blastopore decreases, any two given points on the rim at the start will find themselves closer together at the finish of gastrulation. This process is called confluence. In the case of the dogfish, the diameter of the blastopore (edge of the blastoderm) has to increase considerably until it has grown down and passed the equator of the yolk, whereupon it decreases again.

It is characteristic of these lower vertebrates (fish, frog, and newts), that the rim of the blastopore arises along the margin
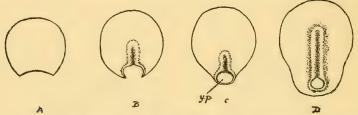
Fig. 114.—Views of the blastoderm of Hypogeophis, one of the Gymnophiona showing the origin and closure of the blastopore. (From Jenkinson, after the brothers Sarasin.)

The anterior edge of the blastoderm here does not become the ventral lip of the blastopore. *yp*, yolk-cells seen through the blastopore.

separating the protoplasmically-rich cells of the animal hemisphere from the cells rich in yolk (or the undivided yolk) of the vegetative hemisphere. Also, that in the closure of the blastopore, the yolk should be enclosed by the growth of the anterior part of this margin which becomes the ventral lip of the blastopore.

This is, however, not the case in the higher forms (reptiles, birds, and mammals), in which there is a primitive streak. In order to understand the evolution of the primitive streak from the simple blastopore of the lower vertebrates, it is necessary to consider the condition in the Gymnophiona, which is more or less intermediate. The quantity of yolk in the Gymnophionean egg brings about the formation of a

blastoderm. The posterior edge of this blastoderm grows back over the yolk and tucks cells in beneath itself, like the typical dorsal lip of the blastopore which it is. Overgrowth also takes place at each side of the dorsal lip, and the blastopore becomes crescentic. Eventually the two horns of the crescent meet and the blastopore is then a closed circle. But the anterior edge of the blastoderm has not moved, it has not grown round underneath the yolk, and it takes no share whatever in the formation of the blastopore. At the same time it is to be noticed that the blastopore is a real aperture, through which the yolk can be seen from the outside. The cavity which communicates with the exterior through the blastopore is, of course, the archenteron, and the lining of this cavity is the endoderm, formed by the activity of the edge of the blastopore.

In the reptiles, yolk is abundant, and cleavage leads to the formation of a blastoderm. At a place which marks the posterior end of the future embryo, cells are proliferated under the blastoderm, forming a lower layer between the blastoderm and the yolk. This lower layer is really the endoderm, which has been formed precociously, probably serving the function of digesting the large quantity of yolk. A dorsal lip of a blastopore arises (not at the extreme hind edge of the blasto-derm, but well within its margin) as a rim beneath which cells become tucked in and passed forwards beneath the blastoderm and above the lower layer. The rim of the blastopore extends to the sides, and so the lateral lips come into being. Eventu-ally the lateral lips extend backwards, and lie parallel to one another. The blastopore is now slit-like, and resembles a primitive streak. The lateral lips of the blastopore join posteriorly, and the blastopore is then closed. The cells which get tucked in by the lips of the blastopore line a cavity which is the archenteron, so that here as in fish, frogs, newts, and Gymnophiona, the blastopore is a real aperture. The archenteron extends far forwards as the result of invagination, and its roof in the middle line becomes the notochord ; on each side the roof becomes mesoderm. The floor of the archenteron fuses with the underlying lower layer and then disappears, so that the blastopore leads right down through

the archenteron to the surface of the yolk. The walls of the definitive alimentary canal are formed from the lower layer,
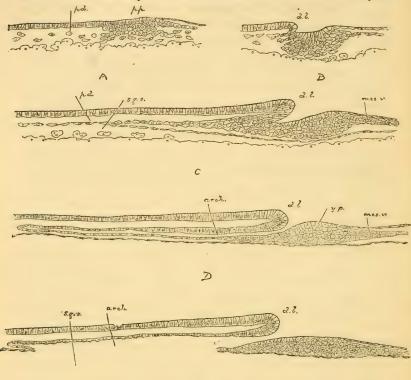
FIG. 115.—Longitudinal sections through the blastoderm of a reptile, showing the origin of the blastopore. (From Jenkinson, after Will.)

A–E, successive stages. A, precocious origin of the endoderm or lower layer (*pd*), which is in contact with the upper layer of the blastoderm at *pp* ; B, origin of the blastopore, *dl*, dorsal lip of the blastopore (*cf*. Fig. 89) ; C, invagination at the blastopore to form the archenteron ; the lower layer forms a continuous membrane separated from the yolk by the subgerminal cavity (*sgc*) ; *mesv*, mesoderm formed from the lip of the blastopore ; D, the archenteron (*arch*) extends a long way forwards beneath the upper layer of the blastoderm ; *yp*, yolk-plug (*cf*. Fig. 75) ; E, fusion of the floor of the archenteron with the underlying region of the lower layer, and their subsequent disappearance, so that the archenteron communicates with the subgerminal cavity.

which is endoderm formed really before the blastopore proper can be said to exist.

The conditions in the reptile lead on easily to those which obtain in birds. Here, again, the endoderm is formed precociously as a lower layer split off from the underside of the superficial layer of the blastoderm. The blastopore, however, never is a real aperture, because its lateral lips are fused together all along their length forming the primitive streak. The dorsal lip is the primitive knot beneath which a solid strand of cells is tucked in to form the notochord. As the primitive streak moves backwards over the blastoderm, it pays in a stream of cells into the hinder end of the notochord. The primitive streak gives off mesoderm to each side. In the bird, therefore, the blastopore is closed from the start, and its aperture is represented only by the depression of the primitive pit just behind the primitive knot, and by the primitive groove which runs along the centre of the primitive streak. The bird's blastopore begins where that of the frog leaves off, for in the latter it will be remembered that the blastopore which was spherical becomes oval, and its lateral lips become apposed to one another, forming what is in fact a short primitive streak. In the bird, there is no invagination, and no archenteron, and the walls of the alimentary canal are derived (as in reptiles) from the lower layer.

In mammals, the embryo develops from a primitive streak. In some cases the blastopore is a real aperture, or in other words, the primitive pit sinks down and opens into an archenteron beneath the superficial layer of the floor of the amniotic cavity (corresponding to the blastoderm). In others, the blastopore is reduced. The primitive streak and archenteron give rise to the notochord and mesoderm, and the endoderm is formed from the lower layer.

In reptiles, birds, and mammals, therefore, the blastopore either closes or arises already closed without the yolk becoming enclosed. For the anterior edge of the blastoderm does not grow down under the yolk to form a true ventral lip of the blastopore.

In Amphioxus where there is little yolk, the rim of the blastopore is formed as the result of simple invagination of the vegetative hemisphere. Thereafter the rim of the blastopore

grows backwards and the embryo increases in length. In Craniates, the quantity of yolk present prevents simple invagination, and the rim of the blastopore arises as the result of overgrowth (epiboly) accompanied by invagination or some form of ingrowth. There is an increasing tendency for the invagination to become reduced as the quantity of yolk increases, and the yolk ceases to become encircled in the process of closure of the blastopore. At the same time, the endoderm appears early (one might say out of its turn), and the aperture of the blastopore becomes virtual.

	Amphioxus.	Frog.	Reptile.	Bird.
Yolk ..	Very little.	Little.	Much.	Very much.
Yolk ..	Enclosed.	Enclosed.	Not enclosed.	Not enclosed.
Gastrulation	Invagination.	Overgrowth and invagination.	Primitive streak and invagination.	Primitive streak, no invagination.
Blastopore	Open.	Open.	Open.	Closed from start.
Gut formed from	Wall of archenteron.	Wall of archenteron.	Lower layer.	Lower layer.

LITERATURE

ASSHETON, R. Growth in Length. Cambridge University Press, 1916.

JENKINSON, J. W. Vertebrate Embryology. Oxford, at the Clarendon Press, 1913.

CHAPTER XVI

THE EMBRYONIC MEMBRANES

The Yolk-sac.—In those forms in which the quantity of yolk contained in the egg is large, the embryo is formed from a blastoderm on the surface of the yolk and does not wait for the latter to be enclosed. So it comes about that the yolk is not situated within the embryo, as, for example, it is in the frog; indeed, in the chick it would be manifestly impossible. In the heavily-yolked forms, then, the yolk is outside the embryo, and it becomes surrounded by a layer of cells which are endodermal and continuous with those of the gut-wall inside the embryo. The yolk then finds itself inside a " yolk-sac," which may be regarded as temporarily extra-embryonic gut. This sac carries a layer of mesoderm outside its (endodermal) wall, and blood-vessels passing between the mesoderm and endoderm absorb the yolk (which has been digested) and convey it into the embryo. Chief among these vessels are the vitelline arteries and veins. Indeed, in most groups of vertebrates, the wall of the yolk-sac is the site of origin of the blood in the form of blood-islands.

In the fish, the function of the yolk-sac circulation is not only to convey digested yolk, but also to oxygenate the blood in its many capillaries, at the early stages of development before the gills have become functional.

The yolk-sac reaches the height of its development in reptiles and birds; and in the Monotremes which, although mammals are oviparous, yolk is present and the yolk-sac is large. What yolk there is in the egg of the Marsupials is

extruded, and the egg of the Placental mammals contains no yolk. Nevertheless, in both the last-mentioned groups a yolk-sac is present although it contains no yolk.

In several groups of vertebrates, the yolk-sac may come to bear interesting relations to the wall of the oviduct, with which it is in contact if the egg is not laid but undergoes development within the body of the mother. The blood-vessels of the yolk-sac are in these cases able to absorb substances from the circulation of the mother (by diffusion), and such an organ of physiological communication between mother and embryo is a placenta. It is necessary to specify the organ which forms the placenta, and a placenta derived from the yolk-sac is called an omphaloidean placenta, to distinguish it from the allantoic placenta which is formed by the allantois.

An omphaloidean placenta is present in the dogfish Mustelus, and in the reptile Chalcides ; it is the chief nutritive organ in the embryonic development of the Marsupials (in fact, it is the only form of placenta in all except Perameles which in addition has an allantoic placenta), and in the " Placental " mammals it arises early and disappears later.

As development proceeds, and the quantity of yolk is reduced, the size of the yolk-sac decreases and finally it is withdrawn into the body through the umbilical stalk.

The Allantois.—The allantois occurs in reptiles, birds, and mammals, and attains its greatest development in the latter. It develops as an outgrowth from the hind part of the gut, and is an endodermal sac covered with mesoderm in which blood-vessels run. In amphibia it is represented by the (allantoic) bladder. In reptiles, birds, and Monotremes, the allantois functions as a respiratory and excretory organ, for which it is well fitted since the excretory ducts open into its base, and its distal portion is spread out close beneath the (porous) shell. In the reptile Chalcides, the Marsupial Perameles, and the Placental mammals, the allantois enters into relations with the wall of the oviduct (or uterus) and forms the allantoic placenta. Its function is then nutritive as well as respiratory and excretory. It is easy to see how this may have occurred in evolution by the retention of the egg within the oviduct and

the disappearance of the shell. It is necessary to mention this last proviso because in some forms the egg is not laid ; it undergoes development in the oviduct but does not lose the shell. This condition, which occurs in the viper, is called ovo-viviparous.

In the Placental mammals, the allantois relieves the yolk-sac in the formation of the placenta, and the higher the order of
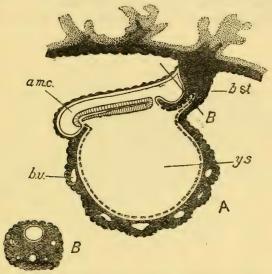
Fig. 116.—Diagram of the relations of the embryonic membranes in the human embryo. (From Jenkinson, after Graf Spee.)

The embryo, developed in the floor of its amniotic cavity (*amc*) is attached to the trophoblast by the mesodermal body-stalk (*bst*), into which the allantois is beginning to grow ; *bv*, blood-vessels round the wall of the yolk-sac (*ys*) B, transverse section through the body-stalk in the plane indicated.

mammals the earlier does this happen. Indeed, in the highest of all, the Primates (including man), the mesoderm of the allantoic stalk appears from the beginning (the " body-stalk "), and the endodermal allantois grows into it later. In these animals the allantoic blood-vessels (the umbilical arteries and veins) are ready at a very early stage to transport to and from the embryo, which increases the efficiency of the placenta. The blood-vessels of the allantois are usually covered by

the outermost layer of extra-embryonic ectoderm, known as the chorion in reptiles and birds, and the trophoblast in mammals.

The Allantoic Placenta.—The blood of the mother and that of the embryo are never in direct communication. The passage of foodstuffs, excretory and respiratory substances must therefore take place by diffusion through the membranes. The efficiency of the placenta is conditioned by the area of mutual contact between the maternal and embryonic circula-
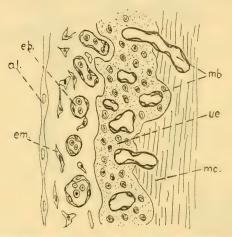
FIG. 117.—Section through a part of the allantoic placenta of Perameles : embryonic tissue on the left, maternal on the right.   (After Hill.)

al, allantois ; *eb*, embryonic blood-vessels ; *em*, embryonic mesoderm ; *mb*, maternal blood-vessels ; *mc*, maternal connective tissue ; *ue*, uterine epithelium (which has become syncytial).

tions, and by the thickness and number of the intervening membranes.   The area of contact can be increased by throwing the surfaces of the maternal and embryonic tissues into folds ; and the intervening membranes can be decreased by removal or erosion of certain of the layers of the uterus.   Four grades of structure and corresponding efficiency can be seen in the mammals, which will now be taken in order.

(i) The embryonic and maternal surfaces are flat and un-folded ; the area of contact is therefore small.   However, the

trophoblast (embryonic outermost layer) disappears, and the uterine epithelium (innermost maternal layer) becomes syncytial and contains blood-vessels. Substances therefore have to pass through the wall of the maternal capillaries, through the uterine epithelium, across the intervening space and through the wall of the embryonic capillaries. This type of placenta occurs in Perameles, the only Marsupial to possess an allantoic placenta at all. It was probably present in the ancestors of the Marsupials, and has been lost in the other living Marsupials.
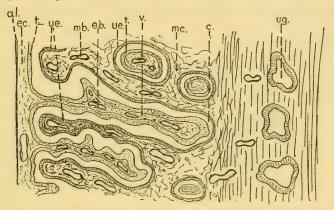
Fig. 118.—Section through a part of the allantoic placenta of the cow ; embryonic tissue to the left, maternal to the right.

The trophoblast (*t*) is produced into villi (*v*), which fit loosely into crypts (*c*) in the uterine wall, the epithelium of which (*ue*) persists ; *al*, allantois ; *eb*, embryonic blood-vessel ; *ec*, embryonic connective tissue ; *mb*, maternal blood-vessel ; *mc*, maternal connective tissue ; *ug*, glands in the wall of the uterus.

(ii) The embryonic and maternal tissues are thrown into folds ; embryonic " fingers " or villi fitting into corresponding crypts in the uterine wall. In the pig, villi are distributed all over the trophoblast, but in the cow they are grouped together in clumps forming cotyledons. The uterine epithelium per- sists. Substances therefore must diffuse through the wall of the maternal capillaries, connective tissue (uterine epithelium), trophoblast, and the wall of the embryonic capillaries.

(iii) The epithelium of the uterus disappears, and the

underlying maternal connective tissue is invaded by the developing villi of the trophoblast, so that the latter comes into contact with the walls of the maternal capillaries. Substances have only to pass through the wall of the maternal capillaries, the trophoblast, and the wall of the embryonic capillaries in order to diffuse through. This type of placenta occurs in carnivora (cat and dog), and is restricted to a zone of the trophoblast, whence its name zonary.

(iv) The epithelium of the uterus is removed, but the underlying connective tissue is not invaded as in the carnivores ; instead the trophoblast is very much thickened and then
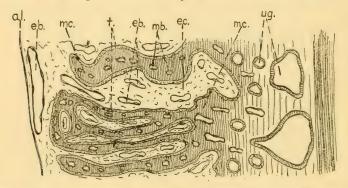
FIG. 119.—Section through a part of the allantoic placenta of the cat ; embryonic tissue to the left, maternal to the right.

Letters as Fig. 118.

hollowed out here and there to form lacunæ. The remaining projections from the trophoblast are called pseudovilli to distinguish them from the true villi which are definite outgrowths. The maternal blood-vessels are " tapped " by the very thorough erosion of the uterine wall, and the blood flows out of them and into the lacunæ in the trophoblast. The pseudovilli are therefore bathed in the blood of the mother, and the substances have only to pass through the trophoblast and the wall of the embryonic capillaries to enter into the embryonic circulation. This is the highest type of placenta, and it is found in the rabbit, mouse, bat, shrew, hedgehog, mole, Tarsius, monkey, and man. It is interesting

to note that these mammals are more closely related to one another than to other mammals. This type of placenta occupies a disc-shaped region of the trophoblast, whence its name discoidal.

At birth, the allantois and placenta are nipped off from the embryo ; and the placenta separates from the uterus, and is expelled as the "after-birth." In the carnivores (type iii) this entails a certain amount of loss of maternal tissue ; in the others the mother only loses blood. In Perameles, on the other hand, the placenta is absorbed by the uterus.

It must be remembered that as well as being an organ of exchange between mother and embryo, the placenta functions during early stages of development as a regulator of metabolism of substances such as glycogen. Later on, this function is taken on by the liver of the embryo.

The Amnion.—The amnion is found only in reptiles, birds, and mammals. All these animals differ from the fish and amphibia in that the eggs are laid on dry land and not in water. The amnion is formed by folds of the extra-embryonic ectoderm and underlying mesoderm which rise up on all sides of the embryo and meet above it. The inner layer so formed enclosing the amniotic cavity is the amnion proper ; the outer layer is the chorion. In the reptiles and the Monotremes, the fusion of the folds above the embryo is not complete, so that the amniotic cavity is not quite closed. In the birds, the amniotic cavity is closed, but it opens again later (at the sero-amniotic connexion).

In the mammals, there are two principal types of amnion-formation. In the one type, of which the rabbit is characteristic, the embryonic plate comes to the surface of the blastocyst by the disappearance of the overlying trophoblast (cells of Rauber), and the amniotic folds rise up on each side of the embryo from the edge of the embryonic plate. This method of formation of the amnion is very similar to that which holds in birds ; the chorion of the latter corresponds to the trophoblast of the mammals. The only difference is the fact that the trophoblast in the mammal forms a complete investment from the earliest stage.

In the other type, of which the mouse is an example, the amnion arises as a cavity hollowed out in the inner mass of cells, within the trophoblast. This method is called amnion-formation with entypy of the germ. In this case, there are no amniotic folds, and the trophoblast (which forms a complete investment, as in the rabbit) does not become interrupted by any disappearance of Rauber's cells. When the amniotic cavity is formed in the mouse, the embryo becomes differentiated on its floor. The mouse therefore starts from a condition which the reptiles do not reach until a fairly late stage of development, when the amniotic folds have been formed.

The amniotic cavity contains fluid, and this enables the embryo to develop in a fluid medium, although its egg was not laid in water.

It is interesting to note how in the higher vertebrates certain processes take place as if they were abbreviations of the conditions which prevail in lower vertebrates. To start with, the primitive streak which is the beginning in higher vertebrates, represents a stage which the lower vertebrates only reach after the blastopore has formed, and become closed by the apposition of its lateral lips. Similarly, the mammal with a hollowed-out amniotic cavity within the trophoblast starts from a condition which the reptiles and birds reach after the upgrowth and fusion of the amniotic folds. Not only this, but in such mammals the amniotic cavity arises first and the embryo forms in its floor ; whereas in the reptiles and birds the embryo forms first and the amniotic folds arise afterwards. This process of " short-circuiting " and telescoping of developmental processes reaches its climax in the Primates, where the body-stalk develops first and the allantois grows into it later. In lower mammals as well as in reptiles and birds, the allantois grows out from the hind gut at a fairly late stage. In the Primates, the conditions are as if everything were first got ready for the embryo, after which it makes its appearance. This is not without interest in connexion with the superior organisation and differentiation of the highest mammals, for this superiority in construction is dependent on a prolonged

and intense period of embryonic development, when the efficiency of the embryonic membranes and placenta is of the utmost importance.

LITERATURE

JENKINSON, J. W. Vertebrate Embryology. Oxford, at the Clarendon Press, 1913.

CHAPTER XVII

THE SKIN, AND ITS DERIVATIVES

THE skin forms the outermost layer of the body, and its functions are protective, excretory, and sensory; for all information which the animal receives concerning the outer world must come through the skin. Correlated with these functions, it is found that the constituents of the skin may undergo various modifications.

The skin is formed of an outer ectodermal layer, the epidermis, and an inner mesodermal layer, the dermis. In Amphioxus the epidermis is only one-cell thick (as in most invertebrates); while in all Craniates it is several layers of cells in thickness. Of these, the innermost form the stratum germinativum (or stratum Malpighi) which constantly produces new cells, while the outermost layers tend to become horny forming the stratum corneum. As the cells become horny the protoplasm within them dies, and they become worn away by friction with the environment and replaced from the stratum germinativum. In many reptiles and amphibia, it is common for the superficial layer of the epidermis (overlying the horny scales) to be sloughed off all at once and replaced.

The epidermis may be ciliated in early stages of development in the lower forms, such as Amphioxus and the frog tadpole.

The epidermis covering the eye becomes very thin and transparent forming the conjunctiva. Sensory cells are present in the stratum germinativum, and it will be remembered that the sensory epithelium of the nose, of the eye, the ear, the lens and the placodes which contribute nerve-cells to the cranial ganglia, are all formed from the epidermis.

The skin excretes by means of glands which may be composed of single cells or many cells. Examples of the latter are to be found in the mammary, sebaceous, and sweat-glands of the mammals. These glands arise in the epidermis and project inwards into the underlying dermis. In some animals the glands may be modified into poison-glands; and in deep-sea fish they may produce a luminous secretion.

The epidermis may be modified into a variety of structures such as horny scales (corneoscutes) which are present in reptiles, birds (chiefly on the feet) and mammals (all over the body of the Pangolin, at the base of the tail of the rat). The epidermis also gives rise to feathers which are characteristic of birds (see p. 224); hairs which are characteristic of mammals (see p. 234); the termination of the digits which may take the form of claws, nails, or hoofs; and the horny covering of the beak in tortoises and birds. The " horns " of cattle are formed of a layer of epidermal horn overlying a central dermal bony core. The horn of the rhinoceros is made of fused hair. Special epidermal structures on the edge of the mouth of Petromyzon, frog tadpoles, and Ornithorhynchus, give rise to the so-called " horny teeth," which have nothing to do with true teeth. Lastly, the epidermis produces the cap of enamel which forms a covering to the dentine of denticles and true teeth.

Hairs and feathers are commonly moulted at intervals and replaced.

The dermis forms the leathery layer of the skin. It contains blood-vessels which serve to supply the cells of the epidermis as well as those of the dermis, and especially the papillæ at the bases of hairs and feathers, and the glands. In amphibia this dermal circulation also serves respiratory purposes, and in the mammals it forms part of the mechanism for regulating the heat of the body. In amphibia the dermis is separated from the underlying muscles by lymph-spaces, but in higher forms the skin is firmly attached to the muscles by connective tissue. In higher forms, special muscles arise in connexion with the dermis. Some of them are attached to scales, feathers, or hair-follicles, which they move. It is

S

by the contraction of these (smooth) muscles in mammals that hair is made to " stand on end," and the puckering of the skin round the hair-follicles gives rise to the condition known as " chicken-skin."

In addition to these dermal muscles, there are in the higher forms, and especially in the mammals, sets of muscles beneath the skin and which move the skin as a whole. The panniculus carnosus muscles are in the region of the trunk and they serve to shake the skin. (They are of somatic origin.) In the head and neck regions the platysma muscles (of visceral origin) move certain parts of the skin such as the lips, eyebrows, and ears. In man, these are the muscles of expression. The smooth dermal muscles are innervated by sympathetic fibres, the panniculus carnosus by ventral nerve-roots, and the platysma by the facial nerve.

Just as the cells of the epidermis seem to be prone to the production of horn and horn-like structures, so the cells of the dermis seem to run to the formation of bone and dentine. Dentine is the substance of which denticles and teeth are formed, under the epidermal cap of enamel. The bone produced in the dermis takes the form of dermal or membrane-bone, bony scales, or fin-rays (lepidotrichia). In Selachii the dermis forms dentine but no bone.

Dermal bones are widely distributed over the body in forms above the Selachii. They play an important part in the formation of the skull, and of the pectoral girdle. In some animals, the body may be entirely covered by an armour of bony plates, as in the Labyrinthodonts, or the armadillos. These bony plates are osteoscutes, and remnants of them are to be found in the carapace and the ventral shield (or plastron) of the tortoise, and in the so-called abdominal ribs or gastralia of Sphenodon, crocodile, Plesiosaurs, Ichthyosaurs, Pterosaurs, and Archæopteryx (see Fig. 160). Osteoscutes are also present in Gymnophiona, lizards, and crocodiles.

In the fish, the dermal bones come into relation with the overlying denticles, forming complex scales. In the Osteolepidoti and primitive (extinct) Dipnoi, the denticles have fused together forming a layer of " cosmin," and this

is attached to the underlying bony plate, which forms the so-called " isopedin " layer. This is the " cosmoid " scale.

In the primitive (extinct) sturgeons (the Palæoniscoidea) and in Polypterus, the layer of cosmin is not only covered by bone underneath (the isopedin), but also on top, the superficial
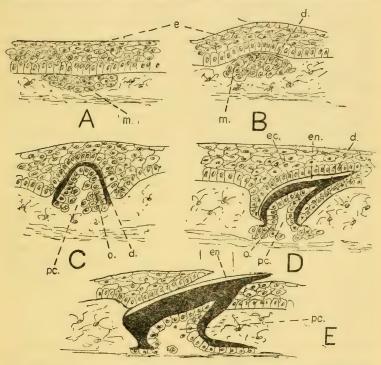
FIG. 120.—Sections through the skin of Scyllium embryos, showing the mode of development of the placoid scales or denticles.

d, dentine ; *e*, ectoderm ; *ec*, modified ectoderm cells which produce the enamel ; *en*, enamel ; *m*, mesoderm ; *o*, odontoblasts, mesoderm cells which produce the dentine ; *pc*, pulp-cavity.

layer of bone being called the ganoin. This type of scale is called palæoniscoid. In Lepidosteus the structure of the scale is similar, but the layer of cosmin has disappeared, and the scale consists simply of a layer of ganoin overlying a layer of isopedin. This is the lepidosteoid type of scale. The palæoniscoid and lepidosteoid scales are of course beneath

the epidermis since the layer of ganoin (bone) is a mesodermal structure. The epidermis overlying these scales may possess true denticles. It is also worth noticing that the structure of the dermal bones and of the dermal fin-rays (lepidotrichia) in a given animal tends to be identical with that of the scales.

In the higher bony fish or Teleosts, the scales lose the layer of ganoin. The scales form in the dermis, but the bone cells become lost and the scales are very thin. It is obvious that these dermal scales together with the dermal scales of Gymnophiona and lizards (osteoscutes) must not be regarded as having anything in common with the epidermal scales (corneoscutes) of higher forms. Dermal scales are retained throughout life ; epidermal scales and denticles are shed.

Other examples of dermal ossifications are to be found in the bone (os corneum) which forms the core of the " horn " of cattle, and which becomes attached to the frontal bone of the skull. Similar little bones form the knobs on the head of the giraffe, while large bony structures in this position give rise to the antlers of deer. Antlers are restricted to the males, they may be forked, and they are shed every year. The size of the antler often bears an interesting relation to the size of the body (see p. 482). Horns, on the other hand, may be present in both sexes, and, except in Antilocapra (the American prong-buck), they are neither forked nor shed.

Lastly, when dealing with the skin, mention must be made of colour. Pigment-cells may occur in the epidermal and the dermal layers of the skin. In some cases, the pigment-cells are capable of altering the distribution of their pigment, with the result that the animal may change colour (as, for example, the frog, or the chamæleon). Pigment may also be present in feathers and in hair, but in these structures the texture of the surface may also produce effects of colour without any pigment being there.

LITERATURE

GOODRICH, E. S. Vertebrata Craniata, Cyclostomes and Fishes. Black, London, 1909.

CHAPTER XVIII

THE TEETH

TEETH and the denticles (or placoid scales) of the dogfish are identical in that they consist essentially of a hollow cone of dentine, inside which is a pulp-cavity, and outside which is a layer of enamel. The dentine is formed from the mesoderm of the skin, and the enamel is produced from the overlying ectoderm. The denticle or tooth is formed below the surface of the skin, and is subsequently erupted through it. In the dogfish the denticles are not restricted to the borders of the mouth, but occur all over the surface of the body. In a few bony fish such as Polypterus, Lepidosteus, and catfish, denticles also occur over the surface of the body ; but in the remainder, and all higher vertebrates, teeth are restricted to the mouth. In addition to those on the premaxilla, maxilla, and dentary, teeth may be carried by the prevomer, parasphenoid, palatine, and pterygoid bones in lower vertebrates ; in the bony fish teeth may even be carried on the branchial arches. In Selachians, the teeth are loosely attached to the underlying skeleton by connective tissue. In bony fish, they are firmly fixed on to the underlying bone by " cement," a modified form of bone, which is absorbed when the tooth is shed. In some cases the teeth may be hinged. In higher forms the bone grows round the base of the teeth, which thus come to lie in grooves (pleurodont) or sockets (thecodont). In Sphenodon and Chamæleo the teeth are fused on to the edge of the bone (acrodont condition) and are not replaced.

The teeth of Osteolepidoti and of the earliest amphibia are peculiar in that their walls are thrown into folds, giving a characteristic appearance when seen in section, and which is
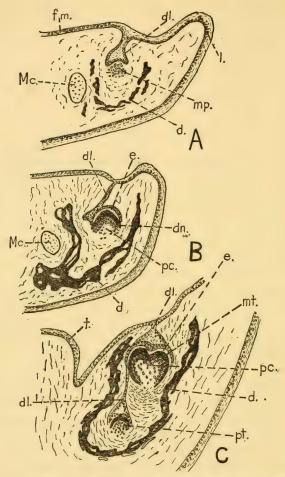
FIG. 121.—Transverse sections through the lower jaw of mammalian embryos showing the development of the teeth.

A, early stage, the dental lamina (*dl*) has grown in from the ectoderm ; B, a tooth-germ has been formed on the dental lamina, the cells of which (ectodermal) produce the enamel (*e*) ; beneath the enamel the mesodermal cells produce dentine (*dn*). C, the development of the first or milk-tooth (*mt*) is nearing completion : beneath it the dental lamina has formed another tooth-germ which will produce a permanent tooth (*pt*) ; the dentary bone (*d*) encloses the teeth in a socket. *fm*, floor of the mouth ; *l*, lip ; *Mc*, Meckel's cartilage ; *mp*, mesodermal papilla ; *pc*, pulp-cavity ; *t*, tongue. (*Cf*. Method of development of the denticle, Fig. 120.)

responsible for the term Labyrinthodontia which is applied to the earliest amphibia. In snakes the teeth may be grooved or even hollow and converted into poison-fangs. The poisonous secretion passes in the groove or tube and is inserted as with a hypodermic needle into the tissues of the prey.

Living Chelonia have no teeth, but they were present in the primitive fossil Triassochelys. The same applies to birds, which are toothless to-day, but which originally possessed teeth, as is shown by the fossil Archæopteryx and others.

The teeth of mammals and of those extinct reptiles which were on the mammalian line of descent differ from those of other vertebrates in that they are not all similar, but differ in
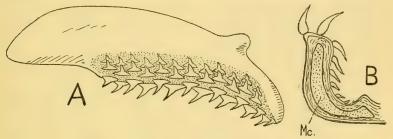
FIG. 122.—The origin of teeth in the dogfish.

A, inner side of one half of the upper jaw, showing the rows of reserve teeth ; B, section through the lower jaw ; the smallest teeth are the most recently formed. *Mc*, Meckel's cartilage.

shape in the various regions of the mouth. This condition is called heterodont, as opposed to the homodont condition when the teeth are all similar.

The most anterior teeth are the incisors, and (except in some Marsupials) they are never more than three in number on each side in each jaw. In the upper jaw they are carried on the premaxilla. Next come the canines, the premolars, and the molars. The molars differ from the premolars in that there is only one set of them, whereas the premolars are represented by a lacteal or " milk " dentition followed by a permanent set which replaces them. In a few mammals, such as the toothed whales, the teeth are all similar, but this is a secondary and degenerate condition.

Another difference between the teeth of mammals and those of other vertebrates lies in the fact that they arise in two sets, or, in other words, they are replaced once only (except for
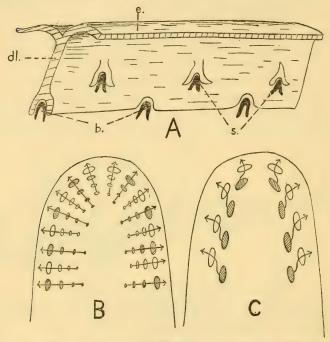
FIG. 123.—Diagrams showing the relation of the mammalian to other modes of tooth-succession. (After Bolk.)

A, diagrammatic view of the outer side of the dental lamina (*dl*) of the lower jaw, showing the alternation between tooth-germs at the side (*s*) and at the base (*b*) of the dental lamina. B, diagrammatic representation of tooth-replacement in reptiles; the teeth formed from the tooth-germs at the side of the dental lamina are shaded: those formed from the tooth-germs at the base of the dental lamina are white; the tooth-germs produce several teeth, which replace other teeth formed originally from the same tooth-germ as themselves. C, diagrammatic representation of tooth-replacement in mammals; each tooth-germ produces one tooth only, and the teeth formed from the tooth-germs at the base of the dental lamina replace those formed from the tooth germs at the side of the dental lamina. *e*, ectoderm.

the molars which are not replaced at all). Other vertebrates have perpetual replacement of teeth as and when the existing ones wear out. The mammalian condition is called

diphyodont, that of other vertebrates polyphyodont. However, it is probable that the two sets of teeth of the mammal are not to be regarded as simply an abridgement and reduction of the many sets of teeth of, say, the crocodile, for the following reason. The ectoderm, which sinks down beneath the surface of the skin of the mouth to produce the enamel, forms a long band extending parallel to the edge of the jaw, known as the dental lamina. The rudiments of the teeth appear on the outer side of the dental lamina in two families ; one from the middle of the side of the lamina, and the other from its base. The teeth formed by one family of rudiments grow up and are intercalated between the teeth formed by the other family. When, in the crocodile, for example, a tooth has been formed, another tooth arises beneath it from the same rudiment, and this second tooth will eventually push out and replace the first. But any given tooth is only replaced by a tooth belonging to its own family, and which has arisen from the same part of the dental lamina. In the mammal there are the same two families of tooth-rudiments, but each rudiment gives rise to one tooth only. Further, owing to the reduction in size of the jaw, there is not room for both families of teeth at the same time. One family appears first, and gives rise to the lacteal or " milk " dentition. Later on, the other family appears and forms the permanent dentition which pushes out and replaces the lacteal teeth. In the mammal, therefore, replacement is effected by a tooth of one family displacing a tooth of the other family ; in the other vertebrates replacement is brought about by the displacement of a tooth by another tooth belonging to the same family. It is probable that the molars belong to the permanent family, the corresponding lacteal teeth having been suppressed.

The Marsupials have a peculiar mode of reproduction in that the young are born very early and in a very undeveloped condition. They are attached to the nipples of the mother and continue their development in her pouch, or marsupium. During this period no teeth are required, and it is found that in Marsupials the lacteal dentition is reduced ; in fact only one tooth (the third premolar) is replaced. That this is a secondary
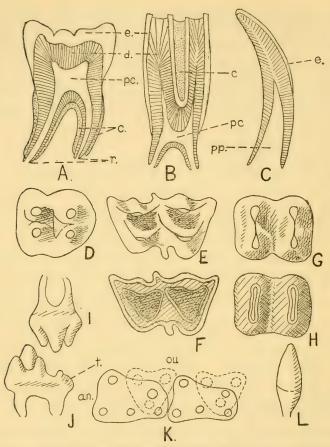
FIG. 124.—Types of teeth (the different teeth are not drawn to the same scale).

A, longitudinal section through a human molar, showing : *c*, cement (here restricted to the base of the tooth) ; *d*, dentine ; *e*, enamel ; *pc*, pulp-cavity ; *r*, roots or fangs ; such a tooth is short and low in the crown, and conforms to the type called brachyodont. B, longitudinal section through a premolar of the horse ; cement, dentine and enamel all enter into the composition of the crown of the tooth, and as the hardness of these substances differs, they are worn away to different extents ; such a tooth is long and high in the crown, and conforms to the type called hypsodont. C, longitudinal section through the incisor of a rabbit, showing the open (" rootless ") pulp-cavity or persistent pulp (*pp*). D, view of the crown of an upper molar of a pig, showing the separate cusps characteristic of bunodont teeth. E, crown of an unworn, F, crown of a worn lower molar of a camel, showing the crescent-shaped ridges joining the cusps, characteristic

reduction is proved by the fact that in extinct forms replacement took place in more of the teeth. There is another point of interest in the teeth of the Marsupials, which refers to the fact that they are the only mammals in which more than three incisors are found on each side. The probable explanation is that in this region of the mouth, the teeth of one family are not replaced by the teeth of the other, but that both families of teeth are erupted together, the members of the two families intercalated as in the crocodile. Behind the canine, however, the families of teeth replace one another as in other mammals. The marsupials, then, are intermediate between the reptiles (simultaneous presence of teeth of both families all over the jaw with complete intercalation) and the higher mammals (no intercalation of teeth of the two families).

The primitive shape of the molar teeth in the mammal is three-cusped or tritubercular in the upper jaw, while those of the lower jaw have three cusps and a posterior " heel " or talonid, and are called tuberculo-sectorial. The three cusps of the upper teeth form a triangle or " trigon," with the apex pointing inwards ; the three cusps of the lower teeth form a " trigonid," with the apex pointing outwards. They are so arranged by this means that the teeth of the upper and those of the lower jaw fit into and work against one another. This type of molar was evolved from the primitive reptilian type in which each tooth had but one cusp. The original cusp is represented by the outer cusp of the trigonid in the lower molars, while in the upper molars the original cusp has been split into two and is represented by the two lateral cusps of the trigon. The remaining cusps and the talonid were subsequently developed in relation to the " fit " of the teeth on one another. The number and arrangement of the cusps may be much modified in the different groups, but the primitive

of selenodont teeth. G, crown of an unworn, H, crown of a worn lower molar of a tapir, showing the transverse ridges joining the cusps, characteristic of lophodont teeth. I, inner side view of a tritubercular (upper) molar, in relation to J, a tuberculo-sectorial (lower) molar ; *t*, talonid. K, diagram of the relative positions of the cusps of tritubercular molars (dotted lines) of the upper jaw, and tuberculo-sectorial molars (full lines) of the lower jaw ; *an*, anterior side ; *ou*, outer side. L, simple peg-like tooth of a reptile.

forms of most groups of mammals have molars of this tri-
tubercular and tuberculo-sectorial type.

When the cusps remain separate as in the pig, the tooth is
called bunodont. In other forms, the cusps may be joined
to one another by ridges running at right angles to the length
of the jaw, as in the tapir (lophodont condition). In others,
again, the cusps are splayed out to form crescents running in
the line of the length of the jaw, as in the camels (selenodont
condition).

It is characteristic of mammalian molars to have divided
roots or " fangs."

Normally, a tooth grows to a certain size (not very big), and
after that the pulp-cavity becomes almost closed at the base.
Such a tooth may have one or more " roots " or fangs, and when
these have formed, the tooth ceases growing. This is the
brachyodont type, the name being derived from the fact that
the teeth are comparatively short, and as a rule their possessors
do not make use of them for grinding hard materials. Where
the diet consists of resistant material which requires grinding,
and in other cases where the teeth are subjected to hard wear,
the pulp-cavity remains widely open at the base, and the teeth
are capable of continuous growth. These teeth are described
as being " rootless," or possessing persistent pulps, and from
the fact that they are usually long, this condition is known as
hypsodont. Examples of hypsodont teeth are to be found in
the premolars and molars of the horse, the incisors of the
rabbit, the incisors (tusks) of the elephant, and the canines of
the boar, to mention only a few.

In the carnivores (cats and dogs) one tooth in each jaw on
each side becomes enlarged and modified for tearing flesh,
forming the so-called carnassial tooth. It is the last premolar
(4th) in the upper jaw and the first molar in the lower jaw.
Other carnivores (bears and seals) do not have the carnassial
tooth well developed.

In addition to dentine and enamel, it is common for the
teeth of mammals to have a complete or partial covering of
bone which is called " cement." This may be restricted to the
roots of the teeth, as in man, or it may form a complete covering

over the crown before the tooth is erupted, as in ungulates. After the tooth has been erupted and projects above the gums, it is subjected to wear, and its different constituents become worn away according to their softness. The hardest substance is the enamel, and next comes the dentine, and lastly the cement which is the softest. The result of the unequal wear in teeth like those of the elephant or of some rodents is that the crown is not smooth but becomes ridged like a file, and such teeth are as efficient as mill-stones grinding against one another.

In some of the Edentates (sloths and armadilloes) the teeth have no enamel, while in others (ant-eaters) and in some whales there are no teeth at all.

There is no difficulty in tracing the teeth of vertebrates back to the denticles of the Selachians, and of some of the Ostracoderms. It has been suggested that denticles also gave rise to dermal bone by fusing together. This is very improbable. Denticles are composed not of bone but of dentine, which differs from bone in that the cells which secrete it do not remain in it but migrate out. Denticles are often found attached to true scales or dermal bones, but these are developed independently from the denticles.

It can be said that the dermal bones and scales develop in relation to the denticles, but not from them.

The so-called teeth of Petromyzon, of Ornithorhynchus, and of the tadpole of the frog are epidermal horny structures, and have nothing whatever in common with the true teeth.

LITERATURE

BOLK, L. Odontological Essays. Journal of Anatomy. Vol. 55, 1921 ; Vol. 56, 1922 ; and Vol. 57, 1922.

MUMMERY, J. H. The Microscopic Anatomy of the Teeth. Henry Frowde and Hodder & Stoughton, London, 1919.

TOMES, C. S. A Manual of Dental Anatomy, Human and Comparative. Churchill, London, 1898.

CHAPTER XIX

THE CŒLOM AND MESODERM

In Amphioxus and all Craniates the most dorsal mesoderm is segmented into somites. These each contain a portion of cœlomic cavity called myocœl, which persists in Amphioxus, but becomes obliterated in higher forms. The median wall of the myocœl is thickened and produces the myotome : a plate of muscle with striated fibres, innervated by somatic efferent fibres (voluntary) through the ventral nerve-roots. The outer layer of cœlomic epithelium lateral to the myocœl gives rise to the dermatome or cutis-layer, beneath the skin. On the median side, the myotome also produces the sclerotome. In Amphioxus this is in the form of a hollow outgrowth, but in higher forms it is composed of mesenchyme. It gives rise in Craniates to the basidorsal and basiventral elements which go to make up the vertebral column.

The dorsal segmented portion of the mesoderm is known as the vertebral plate. The more ventral portion of the mesoderm arises segmentally in Amphioxus, each segment separated from the ones in front and behind by septa. These septa, however, break down, and the ventral cœlomic cavity or splanchnocœl is continuous from end to end of the animal. This condition arises from the first in the Craniates, where the mesoderm in this region, known as the lateral plate, is not segmented. The outer wall of the splanchnocœl becomes applied to the body-wall, and the inner wall covers the gut-wall. The separation between right and left splanchnocœl usually breaks down ventrally, but persists dorsally as the mesentery which suspends the gut. The muscles which the cœlomic epithelium of the splanchnocœl produces are smooth,

involuntary, and innervated by the autonomic nervous system, except for those which are situated in the anterior region of the body, in connexion with the gill-slits. The gill-slits pierce through from the gut to the outside in the region of the lateral plate ; between the gill-slits, in the visceral arches, the lateral-plate mesoderm gives rise to the muscles which move the arches, including the jaws. These muscles are striated and voluntary, but they are not myotomic, and they are innervated by visceral efferent fibres through the dorsal roots of the cranial nerves.

Between the myocœls and the splanchnocœls there are typically little hollow stalks, through which at early stages the cavities of the latter can communicate with those of the former. They are segmental in arrangement. In Amphioxus, these regions of the cœlom represent the future gonads, and are called the gonotomes with their cavities the gonocœls. In the Craniates, they are called the nephrotomes (or intermediate cell-masses) ; the cavities (communications between the myocœls and the splanchnocœl) are the nephrocœls, and they give rise to the tubules of the kidneys and associated structures, eventually losing connexion both with myocœls and splanchnocœl.

In Amphioxus the splanchnocœl is continuous from end to end of the body as in the Ammocœte, for the transverse septum in which the ductus Cuvieri crosses over from the body-wall to the gut-wall, is not large. In Selachians, the transverse septum separates an anterior pericardial cavity from a posterior peritoneal or perivisceral cavity, leaving only very small communications between them in the form of the pericardio-peritoneal canals. In higher forms the separation between pericardial and perivisceral cavities is complete. Beginning in the Dipnoi, the pericardium becomes thin-walled and projects backwards into the perivisceral cavity.

All viscera are morphologically outside the cœlomic cavity and only suspended in it by a bag of cœlomic epithelium which forms a double membrane or mesentery. So the gut is suspended by the dorsal mesentery from the roof of the perivisceral cavity, and between the two membranes composing

it there pass the arteries from the dorsal aorta to the gut. The gut and liver are connected by the lesser omentum, through which the bile-duct runs from the liver to the anterior portion of the intestine. The lungs in amphibia are of course covered
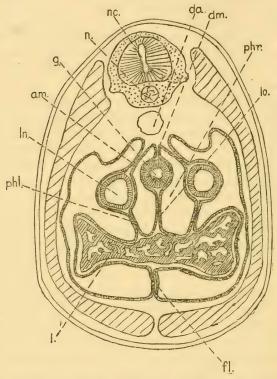
FIG. 125.—Transverse section through the trunk of an embryo of Lacerta, showing the relations of the cœlom.

am, accessory mesentery ; *da*, dorsal aorta ; *dm*, dorsal mesentery ; *fl*, falciform ligament ; *g*, gut ; *l*, liver ; *ln*, lung ; *lo*, lesser omentum ; *n*, notochord ; *nc*, nerve-cord ; *phl*, pulmo-hepatic ligament ; *phr*, pulmo-hepatic recess.

over by cœlomic epithelium (pleura) which is continuous with the ordinary lining of the perivisceral cavity round the stalk of the lungs. In some reptiles, the cœlomic epithelium covering the lung is also attached to the roof of the perivisceral cavity forming the accessory mesentery, and attached to the liver

below by the pulmo-hepatic ligaments.   On each side of the
dorsal mesentery therefore there is a recess, the pulmo-hepatic
recess, bounded on the median side by the dorsal mesentery
and stomach, laterally by the accessory mesentery and pulmo-
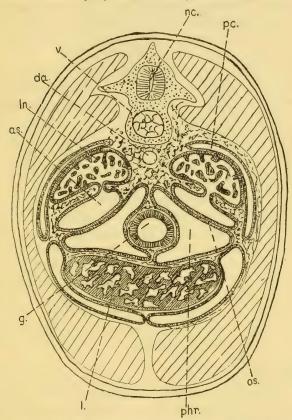
FIG. 126.—Transverse section through the trunk of a bird showing the
relations of the cœlom.

   as, air-sac ; *os*, oblique septum ; *pc*, pleural cavity ; *v*, vertebra ; other
letters as Fig. 125.

hepatic ligament, and below by the liver.   Owing to the
curvature of the stomach and the return of the anterior portion
of the intestine to form the loop of the duodenum, the pulmo-
hepatic recess of the right side comes to form a pocket, the

T

omental cavity. This pocket communicates with the general perivisceral cavity by an opening the front edge of which is formed by the hind border of the accessory mesentery and pulmo-hepatic ligament. Along this edge runs the inferior vena cava. The hind edge of the opening is formed from the dorsal mesentery and lesser omentum and along the latter run the bile-duct, the portal vein and the hepatic artery. The opening is the primitive foramen of Winslow.

In the birds, the conditions start similarly with regard to the accessory mesenteries and the pulmo-hepatic ligaments, but the latter in addition are connected to the side wall of the perivisceral cavity. In this manner the oblique septa are formed, which separate a pair of dorso-lateral pleural cavities (into which the lungs project) from the perivisceral cavity. The latter is further obstructed by the post-hepatic septum which connects the gizzard to the floor of the cavity.

The mammals are characterised by the presence of the diaphragm. This is formed partly from the transverse septum which separates the pericardial cavity from the rest, and partly from cœlomic epithelium in connexion with the mesentery and the folds in which the kidneys hang down from the roof of the perivisceral cavity. By this means the pleural cavities (already separated from the pericardial by the transverse septum) are separated from the remainder of the perivisceral cavity. But it is important to note that the pleural cavities of the mammal are formed in an altogether different manner from those of birds.

Anterior to the diaphragm in mammals therefore there are three cœlomic spaces : the pericardium and the two pleural cavities. The diaphragm contains striped myotomic muscles innervated by the phrenic nerves. Originally the heart and the transverse septum were far forward in the body in the region of the neck, from the spinal nerves of which the phrenic nerve arises. Later in development the heart and transverse septum become shifted backwards, with the result that the phrenic nerves have long courses to run from their origin in the neck to the diaphragm. The diaphragm is pierced by the gut, aorta, and the inferior vena cava.

In many mammals, the dorsal mesentery supporting the stomach from the roof of the perivisceral cavity, becomes
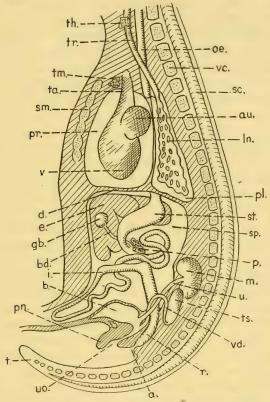
FIG. 127.—Longitudinal section through the trunk of a mammalian embryo, showing the relations of the cœlom and viscera.

a, anus ; *au*, auricle of heart ; *b*, bladder (continuous with allantois) ; *bd*, bile-duct ; *d*, diaphragm ; *e*, liver ; *gb*, gall-bladder ; *i*, intestine ; *ln*, lung ; *m*, metanephric kidney ; *oe*, œsophagus ; *p*, pancreas ; *r*, rectum ; *sc*, spinal cord ; *sm*, sternum ; *sp*, perivisceral splanchnocœl ; *st*, stomach ; *t*, tail ; *ta*, truncus arteriosus ; *th*, thyroid ; *tm*, thymus ; *tr*, trachea ; *ts*, testis ; *u*, ureter ; *uo*, opening of urethra ; *v*, ventricle of heart ; *vc*, vertebral column ; *vd*, vas deferens.

drawn out into a double sheet of cœlomic epithelium which overlaps the transverse colon of the large intestine on the ventral side. Eventually this sheet may fuse with the

mesentery suspending the large intestine (mesocolon). This extension, which is called the great omentum, brings about an increase in size of the omental sac, on the wall of which fat is often deposited.

The Müllerian or oviducts and the uterus are suspended by mesenteries, called mesometria, and which are of interest in determining the relation of the implanted blastocyst to the walls of the uterus. The mesentery supporting the testis is called the mesorchium, that supporting the ovary the mesovarium.

Cœlomic cavities are always lined by mesodermal tissue. In Amphioxus, the cœlomic cavities of the somites, when they arise, are in open communication with the gut, and are hence known as enterocœls. In higher forms, the cœlomic cavities appear as splits in the mesoderm, without communicating with the gut. These cavities are known as schizocœls. The method of origin is not of much importance, but it is important to realise that all cavities which arise, either as subdivisions of, or outgrowths from, enterocœls and schizocœls, are cœlomic. So the cavities of the pericardium, of the kidney-tubules, of the Wolffian and Müllerian ducts, of the gonads in Amphioxus, are cœlomic. On the other hand, no cavity is cœlomic which does not arise in this way. The cavities of the blood-vessels are not cœlomic, although their walls are composed of mesodermal tissue. Cavities lined by tissue other than mesoderm, such as those of the atrium of Amphioxus, nerve-tube, nephridia, amnion, gut, or blastocœl, are, of course, not cœlomic.

The cœlomic cavities originally probably opened to the outside in each segment for the purpose of freeing the germ-cells. Something like this happens in Amphioxus, where also the left anterior head-cavity opens into the preoral pit. Rarely, in higher forms, the cavities of the premandibular somites may open into the hypophysis. Comparable " proboscis-pores " (see p. 360) occur in Balanoglossus and its allies, and in the Echinodermata. In the Craniata, the splanchnocœl may communicate with the outside, through the genital pores via the cloaca as in Petromyzon, through the abdominal pores as in Scyllium, or through the Müllerian ducts.

Mention must be made of the fact that in some cases the electric difference of potential which always accompanies muscular activity has been specially increased, with the result that some muscles have been converted into " electric organs." It is interesting to notice that while in Raia it is the somatic (myotomic) muscles in the region of the tail that have become thus modified, in Torpedo it is the visceral muscles derived from the visceral arches.

The first three pairs of somites (in the Craniates) are small and give rise to the extrinsic eye-muscles. From the fact that they are situated in front of the ear, they are known as prootic somites, and their development is described in Chapter XXVIII. The myotomes which are produced from the next posterior (or metotic) somites are divided by the gill-slits into dorsal and ventral portions, the latter portion forming the hypoglossal muscles.

In Amphioxus, each myotome is a plate of muscle extending from near the middorsal to the midventral line, on one side of the body. When seen from the side, each myotome is bent into the shape of a V with the apex pointing forwards. In Petromyzon, the myotomes behind the region of the gill-slits are like those of Amphioxus ; only the septa are slightly more bent so that each myotome seen from the side is in the form of a W. In fish and all higher forms, however, each myotome behind the gill-slits is divided into two by a horizontal partition or septum. It is in this septum that the " true " or dorsal ribs are formed. The myotomes are then represented by dorsal or epaxonic, and by ventral or hypaxonic muscles.

The muscles of the fins in Craniates are formed from " muscle-buds," which are nipped off from the myotomes.

In the Tetrapods, the epaxonic muscles are much reduced, while the hypaxonic muscles assume greater importance. The muscles of the paired fins and limbs are derived from the hypaxonic portions of the myotomes. Apart from the latter, the great development of which in Tetrapods is connected with the greater strength necessary for locomotion on dry land, the hypaxonic portions of the myotomes also give rise to the

intercostal muscles in the thorax, and the muscles of the abdominal wall.

The simple segmental arrangement of the myotomes which is so characteristic of Amphioxus and lower Craniates, tends to be obscured and lost in the Tetrapods.

With regard to the dermal musculature, the muscles attached to the hair-follicles (arrectores pili) are smooth and innervated by sympathetic fibres. The panniculus carnosus muscles are derived from the striped muscles of the trunk and are therefore innervated by ventral nerves. The platysma muscles, and the muscles of expression are derived from the striped muscles of the 2nd visceral arch, and consequently are innervated by the facial nerve.

LITERATURE

MAURER, F. Die Entwicklung des Muskelsystems und der elektrischen Organe. Hertwig's Handbuch der verg. und exp. Entwicklungslehre der Wirbeltiere. Part 3. Fischer, Jena, 1906.

VAN WIJHE, J. W. Ueber die Mesodermsegmente und die Entwicklung der Nerven des Selachierkopfes. de Waal, Groningen, 1915.

CHAPTER XX

THE skull consists of the protective case round the brain (neurocranium) and of the skeletal supports of the jaws (splanchnocranium). It is formed in all chordates from Petromyzon upwards (whence the name Craniate) and is always cartilaginous at first. In Cyclostomes and Selachians the skull remains cartilaginous throughout life, but in other forms this cartilaginous chondrocranium becomes more or less thoroughly replaced by cartilage-bone, and membrane-bones are added to it. The chondrocrania of the various vertebrates may be compared with one another on the one hand, and on the other, the bony skulls may similarly be compared.

Cartilaginous Skull.—The typical structure of the chondrocranium may now be considered. The floor of the neurocranium is formed of paired trabeculæ in front (enclosing the hypophysial fenestra between them) and of paired parachordals (on each side of the notochord) behind. The auditory capsules are firmly anchored on to the parachordals on each side. Behind the auditory capsules the paired occipital arches rise up from the parachordals, and become attached to the hind part of the auditory capsule. In so doing they enclose a fenestra (metotica) through which the glossopharyngeal and vagus nerves and the internal jugular vein pass. In front of the auditory capsule paired pillars rise up from the parachordals and join on to the orbital cartilages. The latter form the sides of the brain-case in front of the auditory capsules, and the pillars just mentioned are the pilæ antoticæ. The pila antotica joins the front part of the auditory capsule of its own side, and in so doing encloses the trigeminal, facial, and
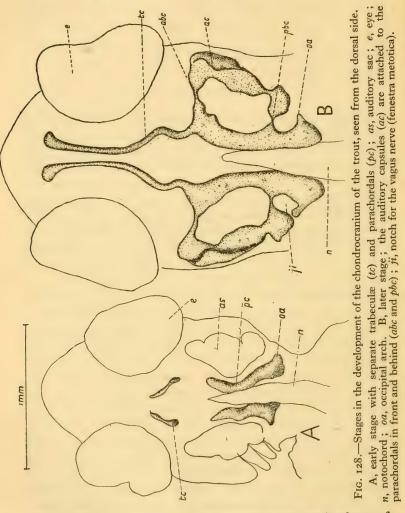
abducens nerves in a fenestra prootica. In front of the pila antotica the optic, oculomotor, and trochlear nerves, and the pituitary vein pass.

FIG. 128.—Stages in the development of the chondrocranium of the trout, seen from the dorsal side. A, early stage with separate trabeculæ (tc) and parachordals (pc); as, auditory sac;, e, eye; n, notochord; oa, occipital arch. B, later stage; the auditory capsules (ac) are attached to the parachordals in front and behind (abc and pbc); jh, notch for the vagus nerve (fenestra metotica).

The olfactory or nasal capsules are formed at the front of the skull. They are separated from one another by the internasal septum formed from the trabeculæ which anteriorly

join together in the middle line. The nasal capsule is separated from the orbit of its side by the lamina orbito-nasalis, which reaches from the trabecula to the orbital cartilage. The roof is often very incomplete, and may be formed only in front and behind. That part of the roof which connects the two auditory capsules is called the tectum synoticum.

The relations of the trabeculæ are of importance, for the hypophysial fenestra which they enclose between them also
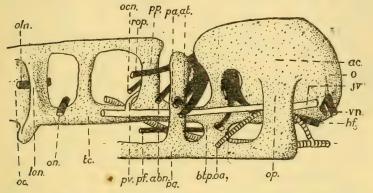
FIG. 129.—Diagram of a schematic chondrocranium seen from the left side, and showing the relations of the cartilages to the principal nerves and blood-vessels.
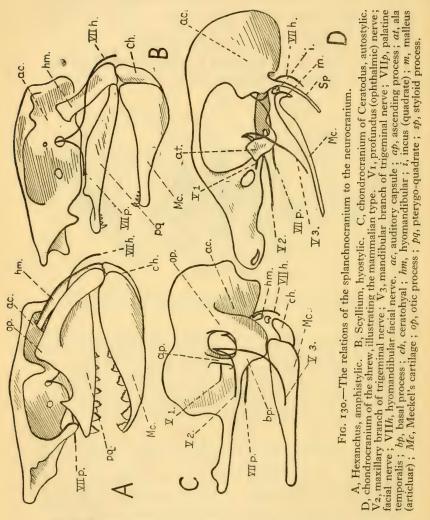
This diagram does not represent any particular form, but shows the type on which nearly all skulls are built. *abn*, abducens nerve ; *ac*, auditory capsule ; *at*, ala temporalis ; *btp*, basal process ; *hf*, hyomandibular facial nerve ; *ic*, internal carotid artery ; *jv*, jugular vein ; *lon*, lamina orbito-nasalis ; *o*, occipital arch ; *oa*, orbital artery ; *oc*, olfactory capsule ; *ocn*, oculomotor nerve ; *oln*, olfactory nerve ; *on*, optic nerve ; *op*, otic process ; *pa*, ascending process ; *pf*, palatine facial nerve ; *pp*, pila antotica ; *pq*, pterygo-quadrate ; *pv*, pituitary vein ; *rop*, profundus ophthalmicus nerve ; *tc*, trabecula ; *vn*, vagus nerve.

serves for the admission of the internal carotid arteries to the brain-case. In those cases where the trabeculæ are wide apart from one another, as in the frog, the skull is said to be platytrabic (or platybasic) ; in others, such as the trout, the trabeculæ are close to one another and fuse in the middle line, and this condition is called tropitrabic (or tropibasic).

The splanchnocranium consists of the pterygo-quadrate of the upper jaw, Meckel's cartilage of the lower jaw, the

hyomandibula and ceratohyal in the hyoid arch, and the cartilages of the branchial arches.

FIG. 130.—The relations of the splanchnocranium to the neurocranium. A, Hexanchus, amphistylic. B, Scyllium, hyostylic. C, chondrocranium of Ceratodus, autostylic. D, chondrocranium of the shrew, illustrating the mammalian type. V1, profundus (ophthalmic) nerve; V2, maxillary branch of trigeminal nerve; V3, mandibular branch of trigeminal nerve; VIIp, palatine facial nerve; VIIh, hyomandibular facial nerve. ac, auditory capsule; ap, ascending process; at, ala temporalis; bp, basal process; ch, ceratohyal; hm, hyomandibular; i, incus (quadrate); m, malleus (articluar); Mc, Meckel's cartilage; op, otic process; pq, pterygo-quadrate; sp, styloid process.

One of the most important features of a skull is the method by which the splanchnocranium is attached to the neurocranium. The hyomandibula is always firmly attached to the

auditory capsule, but with regard to the jaws, there are three types of attachment :

Amphistylic, as in the dogfish Hexanchus, and in Cladoselache. Here the upper jaw has an otic process which abuts against the auditory capsule, and in addition the hyomandibula serves to sling the upper jaw from the neurocranium.

Hyostylic, as in Scyllium. The upper jaw nowhere touches the auditory capsule, and is suspended by the hyomandibula, and ligaments.

Autostylic, as in Ceratodus and higher vertebrates. The hyomandibula takes no share in the suspension of the upper jaw, which is attached to the neurocranium by its own processes.

The processes of attachment of the upper jaw in autostylic skulls are typically three in number. The otic process abuts against the auditory capsule, and lies in front of the main branch of the facial nerve ; the basal process abuts against the floor of the neurocranium, and lies above and in front of the palatine nerve (facial) ; the ascending process rises up on the outside of the pila antotica with which it may or may not join, and lies between the ophthalmic (V1) and the maxillary (V2) branches of the trigeminal nerves.

The autostylic vertebrates above Ceratodus are terrestrial animals which no longer use the gill-slits for respiratory purposes in the adult. So the spiracular cleft gives rise to the tympanic cavity and Eustachian tube, and the hyomandibula becomes the columella auris.

This description of the typical chondrocranium can be applied to most groups of vertebrates. In the mammals an important modification occurs in that the ascending process comes to lie between the maxillary (V2) and mandibular (V3) branches of the trigeminal nerve, and it is usually known as the ala temporalis.

Bony Skull.—Attention may now be turned to the bony skull. The replacing, or cartilage-bones, are fairly constant throughout the vertebrate series. In the neurocranium they surround the brain, the olfactory and auditory capsules ; while in the splanchnocranium they form the main skeletal

supports. The dermal or membrane-bones form a covering just beneath the skin, and in certain regions they line the mouth-cavity. The external covering of membrane-bones is primitively complete, as in Osteolepid fish, and several of them
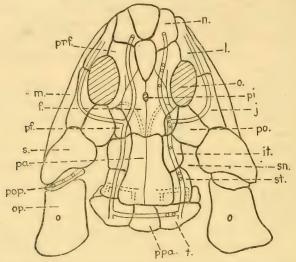
FIG. 131.—Osteolepis : dorsal view of a skull (in the collection of Prof. D. M. S. Watson, F.R.S.), showing the course of the lateral-line canals.

Explanation of lettering for Figs. 131 *to* 149 :

al, alisphenoid ; *art*, articular ; *bo*, basioccipital ; *bpp*, basipterygoid process ; *bs*, basisphenoid ; *c*, canine ; *d*, dentary ; *en*, external nostril ; *eo*, exoccipital ; *ep*, epipterygoid ; *f*, frontal ; *fm*, foramen magnum ; *i*, incisor ; *it*, intertemporal ; *j*, jugal ; *l*, lachrymal ; *ls*, laterosphenoid ; *m*, maxilla ; *mp*, mastoid process ; *n*, nasal ; *o*, orbit ; *oc*, occipital condyle ; *on*, otic notch ; *oo*, opisthotic ; *op*, opercular ; *os*, orbitosphenoid ; *p4*, fourth premolar ; *pa*, parietal ; *pe*, periotic ; *pf*, postfrontal ; *pi*, pineal foramen ; *pl*, palatine ; *pm*, premaxilla ; *po*, postorbital ; *pop*, preopercular ; *pp*, paroccipital process ; *ppa*, postparietal ; *pr*, prootic ; *prf*, prefrontal ; *ps*, parasphenoid ; *psp*, presphenoid ; *pt*, pterygoid ; *pv*, prevomer ; *q*, quadrate ; *qj*, quadratojugal ; *s*, squamosal ; *sm*, septomaxilla ; *sn*, spiracular notch ; *so*, supraoccipital ; *st*, supratemporal ; *t*, tabular ; *tb*, tympanic bulla ; *tp*, transpalatine ; *v*, vomer.

are traversed by the canals of the lateral-line system. In these forms, the only openings in the roof of the skull are the orbits, the chinks through which the spiracles opened, and the median hole for the pineal eye which in fish is situated between the frontal bones. In the higher bony fish or Teleostei, it is

common to find that some of the rectus eye-muscles pass back into a tunnel beneath the brain-case; the so-called eye-muscle-canal or myodome.

In the most primitive amphibia, the membrane-bones also make a complete covering to the skull, for which reason these animals are called Stegocephalia. Many of these bones can be identified with those of Osteolepid fish because they are
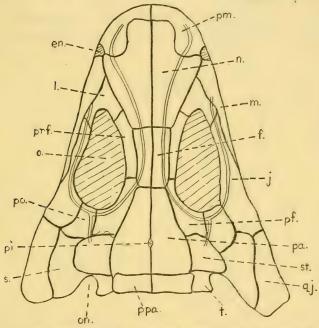
FIG. 132.—Stegocephalian (Loxomma): dorsal view of a skull, showing the course of the lateral-line canals. (Drawn from a cast.)

grooved by the lateral-line system. The only openings in the roof of the skull in the Stegocephalia are the nostrils, the orbits, and the median pineal foramen which in these animals lies between the parietal bones. The spiracles are, of course, closed in land-vertebrates, but the position of their former openings is indicated by a notch in the hind border of the roof on each side.

In land-vertebrates the skull and vertebral column are

separated by a joint, which allows the head to move. The articular facets belonging to the skull which take part in this joint are the condyles. In Stegocephalia there are three such condyles, formed by the two exoccipitals and the basioccipital. In higher forms, as will be seen, the number of condyles may be reduced to one or to two, according as to whether the exoccipitals or the basioccipital (respectively) drop out of sharing in the joint.

In the most primitive reptiles such as Seymouria, the covering of dermal bones is complete, and differs from the
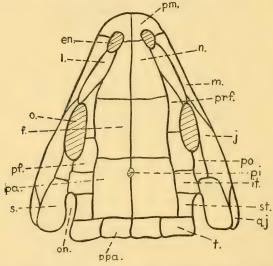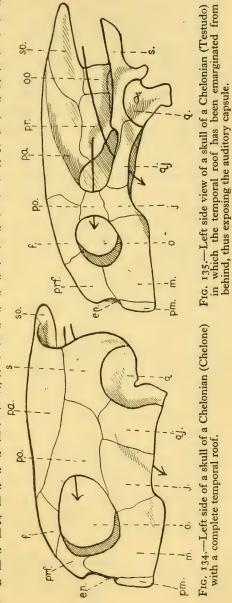
FIG. 133.—Seymouria : dorsal view of a skull. (Drawn from a cast.)

condition of the Stegocephalia only in that there are no grooves for lateral-line canals. As the nature of the roof of the skull is of the greatest importance in regard to classification in the reptiles, it is necessary to consider a few of the relations which the membrane-bones bear to underlying structures. The more median membrane-bones, such as the nasals, frontals, and parietals, overlie the brain-case directly, and form its roof. But the more lateral membrane-bones of the skull-roof, such as the postorbital, supratemporal, and squamosal lie over the auditory capsules. The auditory capsule, formed by the

prootic, and opisthotic (cartilage-) bones lies deep beneath the surface of the skull, with the result that between it and the overlying membrane-bones of the skull-roof there is a space. This space is the temporal cavity; it is continuous in front with the orbit or eyeball-space, and posteriorly the temporal cavity opens on the hind face of the skull by the post-temporal fossa. It must be remembered that the word " cavity " is here used to denote a space which is not occupied by bone; it is, however, not hollow, but filled by the muscles of mastication which actuate the lower jaw. Below, the temporal cavity opens on to the palatine surface of the skull, in front of the auditory capsule, and through this opening the above-mentioned muscles pass. The roof of the temporal region typically has three borders: an

FIG. 135.—Left side view of a skull of a Chelonian (Testudo) in which the temporal roof has been emarginated from behind, thus exposing the auditory capsule.

FIG. 134.—Left side of a skull of a Chelonian (Chelone) with a complete temporal roof.

anterior border which is also the hind border of the orbit ; a lower border, reaching from the maxilla to the quadrate ; and a posterior border which is also the upper border of the post-temporal fossa.

The most primitive reptiles or Cotylosaurs of which Seymouria is an example, are characterised by skulls of this type, in which the temporal cavity is completely roofed over ; a condition inherited from the Stegocephalian ancestors.

In the Chelonia probably the skull was primitively of this kind also, and Chelone is a good example of a skull with a temporal cavity completely roofed over, opening behind by a post-temporal fossa.*   In other forms of tortoises and turtles, however, the roof over the temporal cavity becomes reduced by a process known as emargination.   The skull-roof becomes as it were eaten away from the edge, and this reduction may affect the hind border or the lower border of the roof of the temporal region, or both.   When reduction by emargination has taken place, the prootic and opisthotic bones of the auditory capsule become visible from the dorsal side of the skull.   It is important to notice that in emargination there is no perforation of the skull-roof.

It is common to find the Cotylosaurs and the Chelonia grouped together as Anapsida, since they have skulls completely roofed-over or sometimes emarginated, but never perforated as regards the roof by apertures other than the orbits and nostrils.   These forms usually have three condyles.

The remaining vertebrates are characterised by the fact that the roof of the skull in the temporal region has been perforated, with the result that windows are formed, completely surrounded by bone, and opening into the temporal cavity. A window of this kind is called a temporal fossa or vacuity, and it enables the muscles of mastication to become enlarged. Through the window the auditory capsule is visible.   It must be clearly understood that a temporal fossa is only a perforation

---

* It should be mentioned that some authorities prefer to regard the complete roofing of Chelone as secondarily developed.   This is immaterial for the present purpose, which aims only at pointing out the typical relations of the temporal region of the skull.
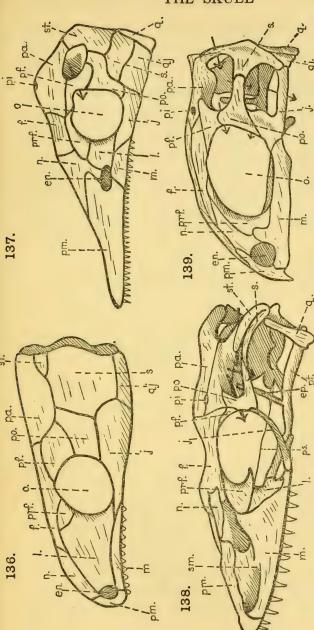
Fig. 136.—Left side view of a skull of a Cotylosaur (Captorhinus), showing the Anapsid type, with the complete temporal roof. (Drawn from a cast.)

Fig. 137.—Left side view of a skull of Ichthyosaurus showing the Parapsid type, with the temporal roof perforated by a superior temporal fossa. (Partly after a reconstruction by Prof. Sollas, F.R.S.)

Fig. 138.—Left side view of a skull of Varanus, showing what is believed to be the Parapsid type with the lower temporal bar emarginated from below.

Fig. 139.—Left side view of a skull of Sphenodon, showing the Diapsid type with the temporal roof perforated by an upper and a lower temporal fossa.

U

in the roof of the temporal cavity, it is not an opening into the brain-case.

Some reptiles have a single temporal fossa on each side. Others have a pair on each side, for which reason they are called the Diapsida. The Diapsida have a superior and an inferior temporal fossa, and these fossæ are separated from the orbit by the post-orbital bar (usually formed by the post-frontal and post-orbital bones) ; they are separated from the post-temporal fossa by the post-temporal bar (supratemporal and squamosal bones) ; and they are separated from one another by the superior temporal bar (post-orbital and squamosal bones. The superior temporal fossa is bordered above by the parietal bone ; the inferior temporal fossa is bordered
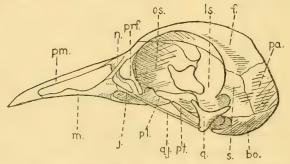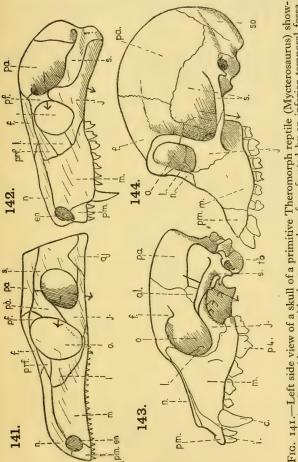
FIG. 140.—Left side view of a skull of a bird (Columba).

below by the inferior temporal bar (jugal, quadrato-jugal, and squamosal bones).

The Diapsida include the Rhynchocephalia of which Sphenodon is an example, the Crocodilia, the Dinosauria, the Pterosauria, and the birds. In the latter, however, the post-orbital and temporal bars have been broken, with the result that the temporal fossæ can no longer be clearly recognised. It can nevertheless be seen that the bird's skull must have been derived from a Diapsid type which had the typical two temporal fossæ. In the primitive crocodiles, in the Pterosaurs, Dinosaurs, and birds, there is also a prelachrymal fossa on each side, between the orbit and the nostril. The condyle is usually single in the Diapsida.

The remaining reptiles have a single temporal fossa on each side, but whereas in some this would seem to be the superior temporal fossa, in others it represents the inferior temporal fossa of Diapsida.

FIG. 141.—Left side view of a skull of a primitive Theromorph reptile (Mycterosaurus) showing the Synapsid type, with the temporal roof perforated by an inferior temporal fossa. (Drawn from a cast.)

FIG. 142.—Left side view of a skull of a late Theromorph reptile (Cynognathus), showing the Synapsid type, with an inferior temporal fossa which has extended upwards and is bordered by the parietal owing to the separation of the post-frontal from the squamosal. (Drawn from a cast.)

FIG. 143.—Left side view of a skull of a dog.

FIG. 144.—Left side view of a skull of a Primate (Chimpanzee), showing the complete separation of the orbit from the temporal fossa.

Forms with a single inferior temporal fossa on each side are called Synapsida, including the Theromorph reptiles and the mammals. The inferior temporal fossa is primitively bounded above by the post-orbital and squamosal bones. In

the higher forms, however, it often happens that the post-orbital and squamosal bones no longer touch one another. The result of this is that the inferior temporal fossa now extends up between them and is bordered above by the parietal bone. From the mere fact that it touches the parietal it must not be mistaken for a superior temporal fossa. This enlarged type of inferior temporal fossa is present in the higher Thero-morph reptiles, and in the mammals. A fossa of this type is also found in the Sauropterygia, or Plesiosaurs. Here again, although the fossa is bordered by the parietal, it is probably an inferior temporal fossa which has extended in the manner just described. For this reason, the Sauropterygia are usually classed as Synaptosauria, close to the Synapsida. Synapsida usually have two condyles.

The Parapsida have a single superior temporal fossa on each side, lying above the post-orbital and squamosal bones, and the supra-temporal bone appears to have been retained. To this group belong the Ichthyosaurs and the Squamata, which latter consist of the Lacertilia and Ophidia. In the Lacertilia, the bar beneath the lateral temporal fossa has been much reduced by emargination from below.* The result of this is that there is very little roofing left over the temporal region, and the quadrate, which still retains the otic process abutting against the paroccipital process of the auditory capsule (see p. 104), becomes uncovered and loose. The quadrate is therefore capable of movement relatively to the squamosal and to the brain-case. This condition, which is called strepto-stylic, is associated with the fact that the upper jaw can move relatively to the brain-case, which arrangement enables the animal to open its mouth with a gape wider than would otherwise be possible.

An extreme case of the streptostylic condition is found in the Ophidia or snakes. Here the postorbital bar and the temporal bar are completely broken down, so that the temporal region is uncovered. The quadrate has lost its connexion with the auditory capsule, and is only indirectly articulated

---

* Some authorities prefer to regard the Lacertilia as derived from Diapsida which have lost the inferior temporal bar.

with it by the intermediary of the squamosal.   When a snake
opens its mouth the lower jaw drops and the quadrate moves
forward.   This movement of the quadrate is imparted to the
pterygoid and transpalatine bones, which, moving forward in
their turn, cause the maxilla and associated bones to rotate
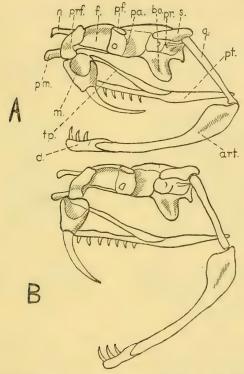
FIG. 145.—Left side view of the skull of a snake (puff adder) showing the
    streptostylic condition of the jaws.   A, with the mouth closed ;   B,
    with the mouth open.

upwards.   In some snakes such as the viper, this process of
rotation of the maxilla is especially interesting, for the maxilla
carries the long teeth which are modified into poison fangs.
When the mouth is open these poison-fangs are made to
project forwards out of the mouth ready for " striking " ;
whereas in the normal position of rest with the jaws closed,

the fangs extend back parallel to and beneath the roof of the mouth.

Streptostylic skulls are also found in the birds, and especially in the parrots. Here the upper beak is freely movable relatively to the brain-case. Some of the Dinosaurs also had streptostylic skulls.

When the quadrate is fixed, and the upper jaw is incapable of separate movement (as in Sphenodon, crocodiles, and mammals, for instance), the skull is described as monimostylic.

In many Theromorph reptiles, as in mammals, it is common for the post-orbital bar to disappear, and the temporal fossa
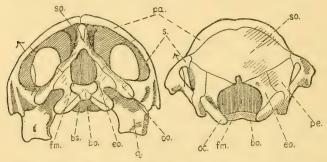
FIG. 146.—Hind view of the skull of Chelone, showing the relations of the post-temporal fossa (through which an arrow is passed into the orbit).

FIG. 147.—Hind view of the skull of Ornithorhynchus, showing the small post-temporal fossa, indicated by an arrow.

then becomes confluent with the orbit. In Ornithorhynchus, for example, the temporal fossa has extended upwards in the manner described above in other Synapsida, and its upper border is formed by the parietal. It is bounded behind by the squamosal, below by the squamosal and jugal (forming the zygomatic arch), and in front it has no border since it is confluent with the orbit. Behind, the temporal fossa of Ornithorhynchus communicates with a small post-temporal fossa between the squamosal and the auditory capsule (periotic bone) and which opens on the hind face of the skull. This is the last appearance of the post-temporal fossa, for in higher mammals it is obliterated, as, for instance, in the dog.

In the higher Primates including man, the post-orbital bar not only persists but actually extends inwards, forming a complete partition between the orbit and the temporal fossa. It may be mentioned that the alisphenoid bone of the mammal is an ossification of the ala temporalis, which corresponds roughly to the ascending process of the pterygo-quadrate of the reptile. The mammalian alisphenoid therefore represents
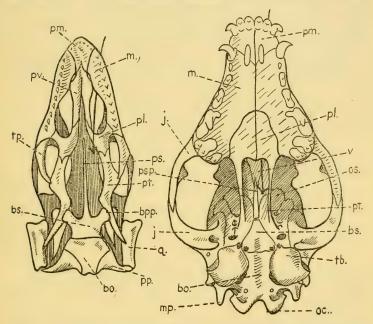
FIG. 148.—Palatal view of a skull of Varanus.

FIG. 149.—Palatal view of a skull of a dog, showing the false palate. An arrow is passed through the nasal passage.

the reptilian epipterygoid, both being really parts of the splanchnocranium. It follows that the so-called " alisphenoids " of fish, reptiles, and birds, which are ossifications of the primitive wall of the brain-case, have nothing in common with the mammalian alisphenoid. Their proper name is laterosphenoid. In birds as in mammals, the brain has undergone great development and enlargement, and so it happens that in the bony

skull certain bones come to form part of the wall of the brain-case although primitively they had nothing to do with it. This applies to the mammalian alisphenoid, and to the squamosal in birds and mammals.

Primitive forms have a large number of bones on the palatal surface of the skull. The pterygoids, of which the fish have three on each side, become more and more reduced in the higher forms. The transpalatine of amphibia and reptiles corresponds to the ectopterygoid of the fish, and it disappears in birds and mammals. In the Tetrapods the pterygoid is a membrane-bone, underlying the pterygo-quadrate cartilage.

The articulation of the pterygoid with the basipterygoid
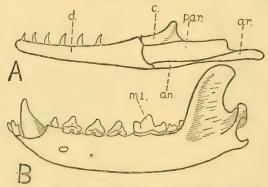
FIG. 150.—Side views of the lower jaws of A, Varanus ; B, a dog. The mammalian lower jaw contains only one bone ; the dentary. *an*, angular ; *ar*, articular ; *c*, coronoid ; *d*, dentary ; *ml*, first molar ; *par*, supra-angular.

process of the basisphenoid, as for instance in Varanus, corresponds roughly to the connexion between the pterygo-quadrate cartilage and the brain-case by the basal process.

In crocodiles, some Theromorph reptiles and in mammals, the maxillæ and palatines have shelf-like extensions which meet in the middle line beneath the original roof of the mouth. These shelves are the false palate, and between it and the original roof of the mouth (formed by the vomer and meseth-moid bones) is the nasal passage leading from the external nostrils to the secondary choanæ. The prevomers of the lower vertebrates are represented by the " dumb-bell-shaped

bone " of Ornithorhynchus. The mammalian vomer represents the anterior part of the parasphenoid of lower forms.

In the lower jaw, Meckel's cartilage ossifies as the articular, and dermal bones are formed round it. In the lower vertebrates these dermal bones are numerous, consisting in the Stegocephalia, for instance, of the dentary, angular, supraangular, splenial, and three coronoid bones. The number of these bones becomes reduced in higher forms. The two halves of the lower jaw in snakes are separate, and their front ends can be moved wide apart. This allows the mouth to be opened very wide indeed, so that the snake is capable of swallowing relatively enormous prey. In some Lacertilia such as Varanus and in the extinct Mosasauria, there is a joint on each side of the lower jaw. These joints enable the space between the two halves of the lower jaw to be widened, and large prey to be swallowed.

In crocodiles, and in the fossil bird Archæopteryx, the lower jaw is characterised by being pierced by a foramen on each side. Among the Dinosauria, the Predentata are peculiar in possessing a predentary bone, the most anterior in the lower jaw. The lower jaw of the Marsupials is characterised by the fact that the lower edge of the hindmost region of each half is bent inwards, forming the " inflected angles."

In all mammals the lower jaw is peculiar in consisting of a single bone : the dentary. Very interesting stages in the reduction in number of bones are found in the Theromorph reptiles. Cynognathus has a large dentary, while the articular, angular, supra-angular, prearticular, coronoid, and splenial are small. The dentary develops an uprising coronoid process which touches the squamosal, and so takes on the function of articulating the lower on to the upper jaw. At the same time the original quadrate-articular articulation (which is present in all lower forms) falls into disuse, and the quadrate becomes small and loose. The next stage is that of the mammals, of which the dog may be taken as an example ; and since here the lower jaw consists of the dentary alone, the question arises as to what has happened to the other bones. The quadrate and articular have been intercalated between the columella auris

and the tympanic membrane, thus forming part of the chain
of three auditory ossicles which is characteristic of mammals.
The columella auris (or hyomandibula), pierced by the
stapedial artery, comes to look like a stirrup and is hence called
the stapes ; the quadrate is now called the incus, and the
articular becomes known as the malleus. At the same time
the angular becomes converted into the tympanic bulla (also
peculiar to mammals) and the supra-angular is represented by
the processus Folii ; the remaining bones of the Theromorph
reptiles have disappeared. It is a striking fact that the
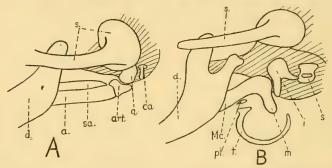
FIG. 151.—Diagrammatic views showing the transition from the reptilian
to the mammalian method of articulation of the lower jaw : A, reptile ;
B, mammal.

a, angular ; *art*, articular ; *ca*, columella auris ; *d*, dentary ; *i*, incus
(quadrate) ; *m*, malleus (articular) ; *Mc*, Meckel's cartilage ; *pt*, processus
Folii (supra-angular) ; *q*, quadrate ; *s*, squamosal ; *sa*, supra-angular ; *st*,
stapes (columella auris) ; *t*, tympanic (angular).

mammalian ear is associated with bones which in the ancestors
served to form the articulation between the upper and lower
jaws. The remarkable change of function which these bones
have undergone is, however, less remarkable than would
appear at first sight, for their essential feature is that they
remain articulated to one another, and so are able to transmit
the vibrations of sound. The columella auris is pierced by
an artery and resembles the stapes in certain lizards and
Gymnophiona, and in the latter group of animals it may be
connected with the quadrate. There is therefore no radical
innovation in the fact that the incus articulates with the stapes.

The most remarkable feature of this change is the fact that it was effected without functional discontinuity. There was never a time when, the quadrate and articular having been drawn away into the service of the ear, the lower jaw had no articulation with the upper, because, before this happened, the dentary had already established connexion with the squamosal. This new squamoso-dentary method of articulation, which is peculiar to mammals, was in working order before the quadrate and articular underwent their modification.

LITERATURE

GAUPP, E. Die Entwicklung des Kopfskelettes. Hertwig's Handbuch der Verg. und Exp. Entwickelungslehre der Wirbeltiere. Part 3. Fischer, Jena, 1906.

GOODRICH, E. S. Vertebrata Craniata. Cyclostomes and Fishes. Black, London, 1909.

GREGORY, W. K. Present Status of the Problem of the Origin of the Tetrapoda. Annals of the New York Academy of Sciences. Vol. 26. 1915.

HUXLEY, T. H. Contributions to Morphology. Ichthyopsida. On Ceratodus forsteri. Proceedings of the Zoological Society of London, 1876.

WILLISTON, S. R. The Osteology of the Reptiles. Harvard University Press, 1925.

TABLE OF VERTEBRATE BONES

Part of Skeleton.		Membrane-bones.	Cartilage- (and tendon-) bones.	Bones of mixed origin.	Cartilage from which the cartilage-bone, or part of the mixed bone ossifies.
Skull	**Neuro-cranium**	Nasal Frontal Parietal Postfrontal = part of Sphenotic Lachrymal Suborbitals Postorbital Intertemporal = part of pterotic ? Supratemporal Squamosal Postparietal Tabulare Prevomer Parasphenoid Vomer = part of Parasphenoid Basitemporal = part of Parasphenoid Septomaxillary	Basioccipital Basisphenoid Presphenoid Exoccipital Supraoccipital Prootic } Peri- Opisthotic } otic Epiotic Mesethmoid Laterosphenoid Orbitosphenoid Turbinals	 Prefontal Sphenotic Pterotic	Basal plate (Parachordal) Basal plate (Parachordal) Trabecular plate Occipital arch Tectum synoticum Auditory capsule Auditory capsule Post-temporal tendon Trabeculæ internasal septum, and nasal capsule Pila antotica Orbital Turbinals Lamina orbito-nasalis Auditory capsule Auditory capsule
	Splanchno-cranium	Premaxilla Maxilla Jugal Quadrato-jugal Ectopterygoid = transpalatine Endopterygoid Pterygoid = Endopterygoid ? Dentary Predentary Angular = Tympanic Supra-angular = Processus Folii Coronoids Splenial Branchiostegal rays Preopercular Opercular Subopercular Interopercular	Quadrate = Incus Metapterygoid Epipterygoid Alisphenoid Articular = Malleus Hyomandibula = Columella auris = Stapes Symplectic Epihyal Ceratohyal Hypohyal Interhyal Basihyal Pharyngobranchial Epibranchial Ceratobranchial Hypobranchial Basibranchial	 Palatine	Pterygo-quadrate Pterygo-quadrate Processus ascendens Ala temporalis Meckel's Hyoid arch Branchial arch Pterygo-quadrate

Part of Skeleton.	Membrane-bones.	Cartilage- (and tendon-) bones.	Cartilage from which the Cartilage-bones ossify.
Axial skeleton (Vertebral Column, etc.)		Neural arch Hæmal arch Hypocentrum Pleurocentrum Radials Ribs	Basidorsal Basiventral Basi ventral Interdorsal and inter-ventral Radials Costals
Appendicular skeleton (Limbs, Girdles, and Sternum)	Post-temporal Supracleithrum Postcleithrum Cleithrum Clavicle	Scapula } Coracoid } Precoracoid } Humerus Radius Ulna Radiale = Scaphoid Intermedium = Lunar Ulnare = Cuneiform Centrale Trapezium Trapezoid Magnum Unciform Metacarpals Phalanges Ilium Ischium Pubis Epipubic = Marsupial Femur Tibia Fibula Tibiale } = Astra- Intermedium } galus ? Fibulare = Calcaneum Centrale = Navicular Endocuneiform Mesocuneiform Ectocuneiform Cuboid Metatarsals Radials Sternum Sesamoids and patella	Scapulo-coracoid Humerus Radius Ulna Carpals Metacarpals Phalanges Ilium Ischium Pubis Epipubic Femur Tibia Fibula Tarsals Metatarsals Radials Sternum Tendons
Dermal skeleton	Lepidotrichia Osteoscutes Gastralia		

CHAPTER XXI

THE primitive skeletal stiffening of the body is the notochord. In Amphioxus this extends to the extreme anterior end of the body ; in Petromyzon it does not reach further forwards than the region of the infundibulum, but in this position it persists throughout life. In the remaining vertebrates, the notochord usually disappears in the skull region.

Surrounding the notochord are two sheaths, the so-called elastica interna and the elastica externa. These are of importance in some forms in connexion with the formation of the vertebral column.

Amphioxus has no structures comparable to vertebræ, but they appear first in Petromyzon in the form of little paired pegs or struts on each side of the nerve-cord, rising up from the notochord. There are two pairs of these pegs to each segment as a rule. The notochord in Petromyzon is continuous and unconstricted, a primitive feature.

A properly formed vertebral column appears first in the Selachii. Each vertebra is composed of a neural arch formed from a pair of basidorsals, and a pair of basiventrals which in the region of the tail form a hæmal arch. Between them, the basidorsals and basiventrals form the body of the vertebra or centrum, which constricts the notochord, and usually obliterates it altogether except between one centrum and the next. Alternating with the basidorsals are the interdorsals, and in some, interventrals are present. The basidorsals and basiventrals perforate the elastica externa and cartilage-cells invade the notochordal sheath. Such centra are called chordal, and they occur in the Selachii, in the sturgeons and in the

Dipnoi. In all other forms the vertebræ arise outside the notochord and do not invade its sheath. These are called perichordal vertebræ.

The vertebræ of the higher bony fish are compact bony structures obliterating the notochord. Amia is interesting with regard to its vertebral column, for in the region of the tail there are what look like vertebræ with neural and hæmal arches alternating with vertebræ without. Those vertebræ with the neural and hæmal arches are the basidorsals and basi-
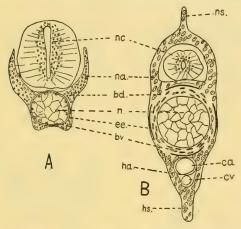
FIG. 152.—Transverse sections through the developing vertebral column of Scyllium embryos.

A, early stage ; B, late stage (in the region of the tail). *bd*, basidorsal *bv*, basiventral ; *ca*, caudal artery ; *cv*, caudal vein ; *ee*, elastica externa ; *ha*, hæmal arch ; *hs*, hæmal spine ; *n*, notochord ; *na*, neural arch ; *nc*, nerve-cord ; *ns*, neural spine.

ventrals ; those without are the interdorsals and interventrals. The neural arches are always formed from basidorsals and the hæmal arches from basiventrals.

The vertebræ are formed from the sclerotome, which is segmented. The anterior part of the sclerotome in each segment gives rise to the interdorsals and interventrals, while the posterior part produces the basidorsals and basiventrals. Later it is found that the basidorsals and basiventrals of one segment fuse on to the interdorsals and interventrals of the

next posterior segment. The vertebræ are therefore inter-segmental in position, which enables the myotomes, which of course are intrasegmental, to be attached to two vertebræ.

The most posterior hæmal arches are enlarged to form the hypurals which support the ventral lobe of the tail-fin.

In the most primitive amphibia, the Embolomeri of the Labyrinthodonts, the vertebræ have neural arches and two
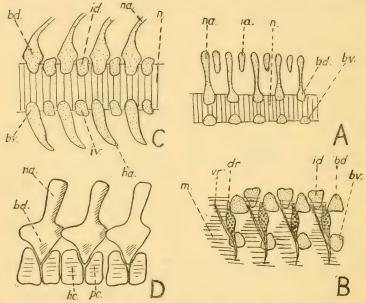
FIG. 153.—Origin of the vertebral column, A, in Scyllium; B, diagram showing the relations of the vertebral elements to the nerves; C, the vertebral column in the tail-region of Amia; D, the vertebral column in the Embolomerous Stegocephalia.

dr, dorsal nerve-root; *hc*, hypocentrum; *id*, interdorsal; *iv*, inter-ventral; *m*, myotome; *pc*, pleurocentrum; *vr*, ventral nerve-root. Other letters as Fig. 152.

centra. The anterior centrum of each vertebra is formed from the basiventrals and is called the hypocentrum; the posterior centrum is formed from the interdorsals and interventrals, and is called the pleurocentrum. While in the later amphibia the hypocentrum has been enlarged and the pleurocentrum reduced, in the reptiles, birds, and mammals the opposite

has occurred, and the vertebræ of these animals have centra which correspond to pleurocentra.   In consequence of this,
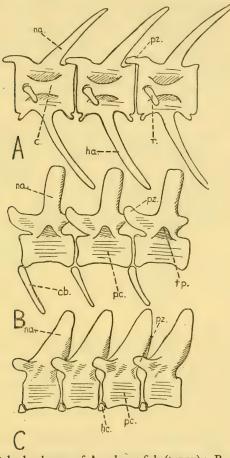
FIG. 154.—Vertebral columns of A, a bony fish (tunny) ; B, crocodile (in the tail-region) ; C, Sphenodon (trunk region).

c, centrum ; *cb*, chevron-bone ; *ha*, hæmal arch ; *hc*, hypocentrum ; *na*, neural arch ; *pc*, pleurocentrum ; *pz*, prezygapophysis ; *r*, rib ; *tp*, transverse process.

the hæmal arches in amphibia are always attached to the centra themselves ; whereas in the amniota, when they occur (mostly in the tail-region), the hæmal arches are attached to separate

x

little elements called intercentra which represent the hypo-centra. These intercentra and hæmal arches in the amniotes are called " chevron-bones " ; they are never found in the amphibia. Primitive reptiles like Seymouria and Sphenodon have a complete set of intercentra all the way along the vertebral column, and some primitive mammals (hedgehog ; mole) have intercentra in the lumbar region.

The transverse processes are lateral extensions of the
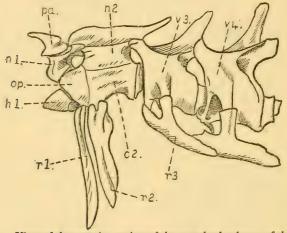
FIG. 155.—View of the anterior region of the vertebral column of the croco-dile seen from the left side.

c2, centrum of the 2nd or axis vertebra ; *h1*, hypocentrum of the 1st or atlas vertebra ; *n1*, neural arch of the 1st or atlas vertebra ; *n2*, neural arch of the 2nd or axis vertebra ; *op*, odontoid peg, or pleurocentrum of the atlas vertebra which has become attached to the axis vertebra ; *pa*, proatlas ; *r1*, 2, 3, ribs of the 1st to 3rd vertebræ ; *v3*, 4, 3rd and 4th vertebræ.

vertebræ from the base of the neural arches. The dorsal (or tubercular) head of the ribs is attached to the transverse process, and in all land-vertebrates except the most primitive Stego-cephalian amphibia (such as Eogyrinus), the transverse processes of at least one vertebra are attached to the ilia of the pelvic girdle forming the sacrum. The sacrum is of course not formed in animals which do not possess hind limbs.

The first vertebra in amphibia is modified to carry the head, and the vertebral column (which in fish is divisible only into

trunk- and tail-regions) is now divisible into regions corresponding to neck, thorax, sacrum, and tail. In the amniotes the first vertebra (the atlas) becomes detached from its centrum, which becomes attached to the second vertebra or axis, and forms its odontoid peg. There are therefore two vertebræ specially modified in connexion with the neck, and a variable number of normal cervical vertebræ which differ from the thoracic in that their ribs are short and do not reach the sternum. The vertebræ between the thoracic (whose ribs reach the sternum) and the sacral are the lumbar. In primitive forms the sacrum affects only one vertebra, to the ribs or transverse processes of which the ilia are attached. In higher forms, and especially in birds, there are several sacral vertebræ.

The vertebræ of land-animals bear facets by means of which they articulate with one another, and so enable the vertebral column to bend with considerable flexibility without diminishing its strength. These facets are the pre- and postzygapophyses. In some groups such as the lizard and snakes, additional facets may be developed. The faces of the centra are either flat or slightly concave or convex, but in the birds a special saddle-like shape has been developed, which allows of very great flexibility.

In the mammals, the number of cervical vertebræ is seven in all species with only three exceptions. These are the Edentates Bradypus which has nine, and a species of Cholœpus which has six or seven, and the Sirenian Manatus which has six.

Ribs are extensions of the basiventrals, and they may be of two kinds. Those which pass just on the outside of the splanchnocœlic cavity are pleural or ventral ribs, and they occur in Dipnoi. "True" or dorsal ribs pass in the horizontal septum which separates the myotomes into dorsal and ventral portions, and they occur in Selachii and in the Tetrapods. Both kinds of ribs are present in Polypterus and some Teleosts.

In the land-vertebrates, the ribs primitively articulate with the vertebræ by a broad head which touches the centrum and the neural arch. These holocephalous ribs as they are termed are present in Labyrinthodonts, Cotylosauria, and Sphenodon.

Later, that portion of the head which touches the centrum (capitulum) became distinct from that which abuts against the transverse process (tuberculum), by the reduction of the intervening part of the head. In this way, the typical double-headed or dichocephalous ribs arose. Between the two heads of the rib and the vertebra there is a canal through which the vertebral artery passes ; and this vertebrarterial canal is conspicuous in the cervical vertebræ on to which the cervical ribs are usually fused.

In many forms, the articular heads of the ribs are degenerate and either the capitulum or the tuberculum may be lost. This
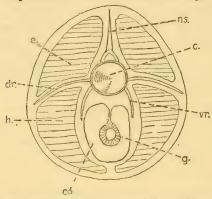
FIG. 156.—Diagram showing the relations of dorsal (" true ") and ventral ribs, as seen in transverse section.

c, centrum of vertebra ; *co*, cœlom ; *dr*, dorsal rib ; *e*, epaxonic muscles ; *g*, gut ; *h*, hypaxonic muscles ; *ns*, neural spine ; *vr*, ventral rib.

secondary single-headed condition must be distinguished from the primitive holocephalous type.

In the Chelonia, the ribs are expanded into broad flat plates which touch one another and are fused to the dermal bones (osteoscutes) to form the carapace. In Sphenodon, crocodiles and in birds the ribs bear uncinate processes, which extend backwards and overlap the next posterior rib. In many cases, the ribs are in two portions : a dorsal or vertebral, and a ventral or sternal portion. The hindmost ribs do not usually reach the sternum, and they are known as floating ribs. Primitively, all the vertebræ as far back as the middle of

the tail bore ribs. In higher forms they do not extend behind the sacrum.

The sternum first appears in Amphibia. It arises from paired rudiments of cartilage which may become replaced by cartilage-bone. In the Amphibia which are alive to-day, the sternum has no connexion with the ribs. The sternum in the Amniotes is however connected with the ribs, and this was probably the condition in the Stegocephalia also. The sternum is also usually in contact with the coracoids and clavicles. In the mammals, the sternum is often broken into a number of pieces or sternebræ. In the birds (with the exception of the Struthiones : ostrich and its allies) the sternum bears a median projection forming the " keel " or carina to which the flight muscles are attached. Analogous but not homologous keels are developed on the sterna of Pterosaurs and bats.

Overlying the sternum on the ventral side there is in many forms a dermal bone, the interclavicle. It is present in the Stegocephalia but has been lost in the living amphibia. Among the reptiles, it is present in all except the snakes. In birds it is apparently absent, unless it is represented by the keel of the sternum. Only the Monotremes preserve the interclavicle among the mammals.

CHAPTER XXII

FINS AND LIMBS

THE most primitive chordates relied for their locomotion on the myotomes of the body-wall, which, by contraction on one side and relaxation on the opposite side of the body, can produce the sinuous bendings which pass like waves down the length of the body and propel the organism along. Amphioxus is in this condition.

Improvement of methods of locomotion is connected with the formation of extensions of the body in the shape of fins. The earliest of these to arise were apparently those which lie in the middle line of the dorsal and ventral surfaces : the so-called median fins. In Amphioxus they are foreshadowed, but in Petromyzon well-developed median fins are present, supported by cartilaginous radials provided with radial muscles at their base on each side. Fish likewise have median fins, and these show an advance over the conditions in Petromyzon in that the web of the fin is supported by dermal fin-rays in addition to the cartilaginous radials. These fin-rays are horny (ceratotrichia) in the Selachians ; bony and jointed (lepido-trichia) in the Teleostomes, and in the Dipnoi they are fibrous and jointed (camptotrichia). The median fins of the amphibia have neither cartilaginous radials nor dermal fin-rays at all, and in some of them the fins develop and regress according to the season and the breeding period.

In the fish, in addition to the median fins there appear the two pairs of " paired " fins : a pectoral pair and a pelvic pair.

The method of origin of median fins and paired fins is very similar. In each case a longitudinal fold of skin appears,

and into it little " muscle-buds " make their way, having been
formed from the myotomes and separated off from them.
Cartilaginous radials then appear, and on each side of these,
the dermal fin-rays.   The fins contain structures derived from
several segments of the body, and this is reflected in the number
of radial muscles, cartilaginous radials, dermal fin-rays and
nerves which the fin contains.

In the most primitive forms, and in early stages of develop-
ment of other forms, it is common to find that the median
fins are continuous and form one fold which extends down the
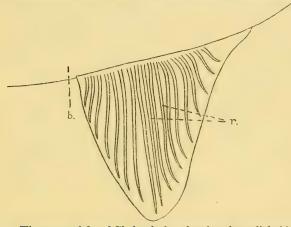
FIG. 157.—The pectoral fin of Cladoselache, showing the radials (r) project-
ing parallel to one another and perpendicular to the side of the body (b).
(Drawn from a cast.)

dorsal side, round the tail and forwards again on the ventral
side.   The presence of a number of separate and discontinuous
median fins in many fish is therefore probably due to the sub-
division of an originally continuous fin.

If the median fin was primitively continuous, it is possible
that the paired fins also were originally continuous folds on
each side of the body, and that they became subsequently
divided into pectoral and pelvic sections.   The fact that in
some fish such as Scyllium, there is in early stages of develop-
ment a continuous series of muscle-buds given off from all
the segments of the trunk makes this possibility fairly probable.

Later on during development the muscle-buds between the positions of the pectoral and pelvic fins come to nothing.

The most primitive paired fins known are probably those of the fossil Cladoselache, in which they are triangular flaps with the apex pointing outwards and the broad base attached to the side wall of the body. The radials are more or less parallel to one another and stick out at right angles to the side of the body. It is important to notice that the radials are scarcely concentrated at all at their base ; in fact the base is the broadest part of the fin. In the body-wall there are some basal cartilages with which the bases of the radials articulate.

The next step in the evolution of the fins was probably the concentration of the radials at the base of the fin. The result of this was that the stalk attaching the fin to the side of the body became narrow, and the fin became free to move in a greater variety of manners. The arrangement of the radials was now in the shape of a fan as in the Osteolepidoti, and the fin itself was in the form of a blunt paddle. The centremost radials formed what may be called the axis of the fin, but this is not well marked in primitive forms in which the fin is short.

By a lengthening of the axis a pointed laurel-leaf-shaped fin is arrived at, like that of Ceratodus (the so-called archipterygium). This type of fin is also present in the fossil Pleuracanthus, where it would seem to have evolved independently from that of Ceratodus. The skeleton of the paired fins of the primitive fossil Dipnoi resembles that of the Osteolepidoti.

On the other hand, by a shortening of the axis and reduction of the radials, the web of the fin comes to be supported mostly by the dermal fin-rays, and this is the condition of the higher bony fish.

The pectoral and pelvic girdles must have arisen in accordance with the need for a firm point of attachment of the fins in the wall of the body. The radials at the base of the fin have fused together and grown inwards, and in so doing they may enclose in foramina the nerves supplying the fin. In the pectoral girdle it is usual to find a dorsal scapular and a ventral coracoid element ; the pelvic girdle is not so well

developed. These girdles lie in the body-wall and are not primitively connected with any other part of skeleton.

In the bony fish, the scapula, coracoid and pelvis ossify as cartilage-bones, and in addition, a number of dermal bones arise in connexion with the pectoral girdle. In a primitive bony fish like Polypterus, these dermal bones are the clavicle, cleithrum, supra-cleithrum, and the post-temporal which is attached to the hind part of the skull. This girdle, which is composed of dermal bones, may be called the clavicular girdle,
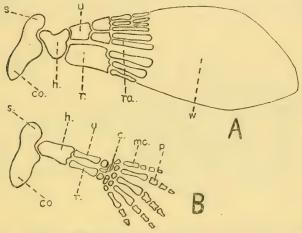
FIG. 158.—Comparison between the fin of Sauripterus, A, and a pentadactyl limb, B. (A after Gregory.)

c, carpals ; *co*, coracoid ; *h*, humerus ; *mc*, metacarpals ; *p*, phalanges ; *r*, radius ; *ra*, radials ; *s*, scapula ; *u*, ulna ; *w*, web of the fin, supported by lepidotrichia. The fin of Sauripterus is an example of the blunt paddle-shaped type of fin.

to distinguish it from the other girdle, formed of cartilage or cartilage-bones, to which the term scapular girdle may be applied. The clavicle is present in the sturgeon (Acipenser), but in all higher fish it is lost. It may seem curious that the pelvic girdle never has any additions of dermal bones to the cartilage-bones of which it is composed. The explanation is that the dermal pectoral girdle originally had no connexion with the pectoral fins. It provides a firm attachment for the muscles of the body-wall just behind the gill-slits in those forms (the

bony fish) in which the gill-slits are highly developed. The gill-slits occupy a region of perforation and weakness, and they prevent the main mass of the lateral body-wall muscles from becoming attached to the skull. The dermal pectoral girdle, which itself is attached to the skull, gives these muscles something solid to work from. The joining of the scapular and clavicular pectoral girdles is due to the fact that both are situated close behind the gill-slits. Since there are no gill-
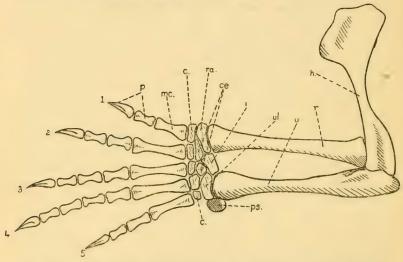
FIG. 159.—The forelimb of Sphenodon : an example of a typical pentadactyl limb with a primitive carpus.

The figures indicate the ordinal numbers of the digits. *c*, carpals of the distal row, which are five in number ; *ce*, centralia ; *h*, humerus ; *i*, intermedium ; *mc*, metacarpal ; *p*, phalanges ; *ps*, pisiform ; *r*, radius ; *ra*, radiale ; *u*, ulna ; *ul*, ulnare.

slits or other source of weakness near the pelvic girdle, the latter has no dermal elements added to it.

From the nature of the water in which they live, the fins of fish are necessarily more or less like paddles. But it is from such paddles (or ichthyopterygia) that the five-digited or pentadactyl limb (cheiropterygium) of the Tetrapods or land-vertebrates was evolved. It is interesting to inquire into the question as to which type of fin most probably gave rise to the

limb. The most convenient starting-point is the blunt lobate fin of the Osteolepidoti (and primitive Dipnoi) with a single large radial at its base, and an increasing number of radials arranged fanwise running to the outer border of the fin. In such a form as Sauripterus (one of the Osteolepidoti) the single basal radial of the pectoral fin may perhaps be held to represent the humerus, and the next two correspond to the radius and ulna of the terrestrial fore limb. In a general way the next radials represent the carpals and metacarpals.

The earliest limbs probably had more than five fingers, and the number of rows of radials in the distal part of the fins
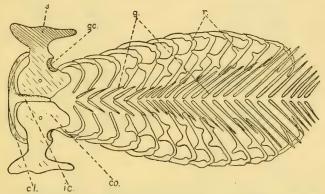
FIG. 160.—Ventral view of the abdominal ribs or gastralia, and pectoral girdle of Sphenodon.

cl, clavicle ; *co*, coracoid ; *g*, gastralia ; *gc*, glenoid cavity ; *ic*, inter-clavicle ; *r*, ribs (true) ; *s*, scapula.

of Sauripterus is greater than five. But if the pectoral fin of Sauripterus be compared with the arm of a primitive amphibian like Eryops, it is easy to see how the structure of the latter could be derived from that of the former. The evolution of the five-digited, or pentadactyl limb is an adaptation to locomotion on land. During this transformation, the limb-girdles must have become better developed, for an animal in air is relatively heavier than in the water, and the limbs are subjected to greater strains and stresses. At the same time, the girdles of the earliest land-vertebrates closely resemble those of their aquatic ancestors. So in Eogyrinus (fossil

Amphibian of the Carboniferous period), the clavicular pectoral girdle is represented by the clavicle, cleithrum, supra-cleithrum and post-temporal, which latter is attached to the hind end of the skull, just as in bony fish. To these is added a median ventral interclavicle. As in all Tetrapods, the scapula (cartilage-bone of scapular girdle) rests on, but is not attached to, the ribs. The pelvic girdle of Eogyrinus is interesting in that the ilium rests on the ribs without fusing with them to form a sacrum. In this respect, the pectoral and pelvic girdles are similar, but in higher forms the ilium becomes firmly attached
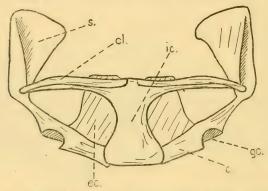
FIG. 161.—Ventral view of the pectoral girdle of Ornithorhynchus. *ec*, epicoracoid (or precoracoid). Other letters as Fig. 160.

to one or more sacral vertebræ. In addition to the ilium, the pelvic girdle contains the pubis and ischium.

In the earliest land-vertebrates, the function of the limbs was not to support the body of the animal but to row it along while its ventral surface rested on the ground. Such movement must have been slow, and improvement came in the reptiles, in which the limbs lift the body off the ground. In them, there was no friction to be overcome between the body and the ground, and the higher the body was lifted, the longer the limbs, the longer the stride and the faster was the pace. In the reptiles the clavicular pectoral girdle is reduced to the clavicle and interclavicle (the cleithrum persists only in some primitive forms), while the scapular girdle usually consists

of a dorsal scapula and a ventral coracoid. In the Theromorph reptiles the scapular girdle may have two ventral elements, the coracoid and precoracoid. In the pelvic girdle the ilium becomes attached to the sacral vertebræ, and the ischio-pubic foramen appears between the pubis and ischium. In some Dinosaurs a post-pubis is present, extending back beneath the ischium. In Chelonia, the pectoral and pelvic girdles have a peculiar position in that they lie inside the ribs, instead of outside them as in other forms. In birds, the pubis rotates
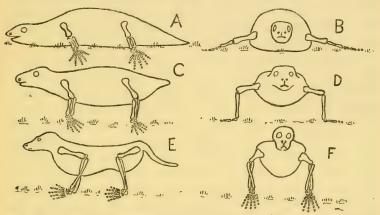
FIG. 162.—Diagrams illustrating the evolution of the limbs of Tetrapods.

A and B, views of the early stage when the limbs stick out laterally and the ventral surface of the body rests on the ground. C and D, later stage, when the body is lifted off the ground, the forearm and shank being vertical, and the limbs projecting to the side. E and F, late stage, when the hind limb is rotated forwards from the acetabulum, and the fore limb rotated backwards from the glenoid cavity ; but the hand points forwards and the radius and ulna are crossed.

backwards and comes to lie parallel to and beneath the ischium, with which it may to a certain extent fuse.

In mammals, the coracoid, precoracoid, and interclavicle are retained only in the Monotremes. The pelvic girdle of Monotremes and of Marsupials is characterised by the presence of a pair of epipubic bones, which support the pouch, or marsupium. The clavicle is often missing in the higher mammals, and especially those which use their limbs for fast running. So the clavicle is absent in the horse, and it is much reduced

in the dog.   In the more primitive forms, and those which are specialised for tree-climbing and digging, the clavicle is usually present.

The limbs themselves show interesting modifications.   In the earliest Tetrapods, the limbs stuck straight out at right angles to the side of the body.   When the ventral surface of the body became lifted off the ground, the upper arm and thigh stuck straight out laterally and horizontally ; at the elbow and knee there was a right-angle bend, so that the forearm and shank descended vertically to the ground.   At the wrist and ankle, there was another right-angle bend, so that the hand and foot extended horizontally away from the body.

In the mammals, starting from the condition just described, the limbs have undergone a rotation.   The hind limbs have been rotated forwards, so that the thigh runs forwards from the hip-girdle, and parallel with the side of the body, the shank runs downwards, and the foot points forwards again.   In the fore limb, however, the upper arm has been rotated backwards parallel with the side of the body, and the forearm runs downwards.   But the hand would point backwards if the fore limb had undergone a simple rotation similar to that of the hind limb (though in the opposite direction).   As a matter of fact, the hand points forwards, and this is brought about by a rotation of the wrist through 180° about a vertical axis which coincides with the forearm.   So it happens that the forearm is twisted, and the radius runs from the outer side of the elbow to the inner side of the wrist, passing in front of the ulna, which runs from the inner side of the elbow to the outer side of the wrist.   This is the typical position (of pronation) in mammals ; most Primates, including man, however, are able to uncross the radius and ulna and so turn the palm of the hand upwards (supination).

It is impossible to go into all the types of limb-structure, but it is interesting to consider the adaptations of limbs to the three great media, viz. to locomotion on land, in the air, and in water.

The fingers and toes of land-living vertebrates above the amphibia end in horny claws which may be modified into

nails or hoofs. When the whole surface of the hand or foot is applied to the ground, as in the human foot, the animal is said to be plantigrade. Other animals, like the dog, rest only the under surface of the fingers and toes on the ground, while the palm of the hand and sole of the foot take no share in
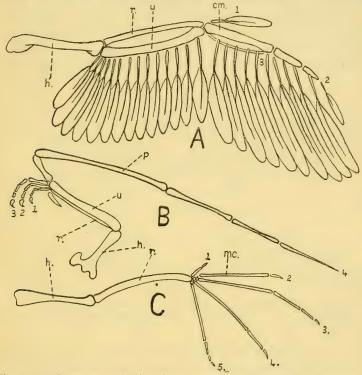
FIG. 163.—Convergence in the adaptation of limbs for flight, A, in birds ; B, Pterodactyls ; C, bats.

cm, carpo-metacarpus ; h, humerus ; mc, metacarpal ; p, phalanx ; r, radius ; u, ulna.

bearing the animal's weight. This is the digitigrade condition. Others again, such as the horse and cow, which rest only on the end joints of the fingers and toes, are unguligrade. [The latter form part of the order Ungulata.]

The limbs of the horse are specialised for rapid movement on hard ground. Only the 3rd digit is retained, and its

extremity is expanded and surrounded by the nail which gives rise to the hoof. The other digits have disappeared, leaving only small vestiges of the metacarpals and metatarsals (of the 2nd and 4th digits) in the form of "splint-bones." The fossil ancestors of the horse show different stages in this process of reduction of the number of digits, and lead back to normal pentadactyl animals. These odd-toed Ungulates are called Perissodactyls. Curiously enough, a parallel process of reduction in number of digits, and of formation of hoofs consisting of a single digit, went on in a group of animals (all
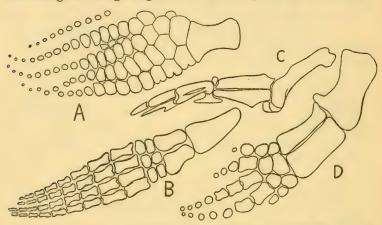
Fig. 164.—Convergence in the adaptation of limbs for swimming, in, A, Ichthyosaurs; B, Plesiosaurs; C, birds (penguin); D, mammals (dolphin).

now extinct) quite independently of the horses : the Thoatheria. This is a very remarkable case of convergence in evolution.

In the "cloven-hoofed" Ungulates or Artiodactyls, the hoof is formed from the end joints of digits 3 and 4, as in cattle, where the metacarpals and metatarsals of the two digits fuse.

Among mammals, limbs with a primitive type of structure are those of the Primates, which preserve all the five digits. In most Primates, the first digit (thumb or big toe) is capable of touching any or all the remaining digits, i.e., is opposable. This structure enables the limb to grasp objects firmly. Apes

have this power in feet as well as hands, while man only preserves the capacity to oppose the first digit in his hands.

Three separate and independent groups of vertebrates have become adapted to life in the air, by the modification of the fore limbs into wings. These are the extinct Pterosauria (" flying reptiles "), the birds and the bats. In the Pterosauria, the fourth digit of the hand was enormously elongated, and a web of skin was stretched between it and the side of the body, extending back to the hind limbs and tail. The bird's wing is built on an altogether different principle, for the wing-surface is made up of a number of feathers inserted on the hand and forearm. The skeleton of the forelimb of the bird shows a reduction in number of digits to three, and the claws at the end of the digits have disappeared except in the young of some birds, such as the ostrich and of the Hoatzin. The primitive fossil bird Archæopteryx had well-developed claws.

The wing of the bat is different, again, for in it the 2nd, 3rd, 4th, and 5th digits of the hand are much elongated, and support a web of skin which stretches out from the side of the body.

The three types of wings just described form another interesting example of convergent evolution on the part of unrelated animals, but the most striking example is that furnished by the limbs of those land-vertebrates which have subsequently returned to an aquatic mode of life and become adapted to it. The adaptation takes the form of a modification of the limbs into flippers or paddles, which superficially may come to resemble the fins of fish, but which betray their descent from the pentadactyl structure of the land-vertebrate's limb in their internal structure. This adaptation has taken place at least nine separate times, in independent groups. Three of these are mammals : the whales, the Sirenia, and the seals. Among the birds, the penguins have modified the wing into a paddle. In the reptiles, the turtles (Chelonia), Ichthyosaurs, Plesiosaurs, Mosasaurs, Thalattosuchia, and Thalattosaurs all show the same modification of the limbs into paddles, and in several fossils it is possible to trace the evolution from normal pentadactyl limbs.

In the more highly modified of these paddle-like limbs (as in the whales, for example), it is common to find that the number of phalanges is increased (a condition known as hyperphalangy). In the broad paddles of Ichthyosaurs, the number of rows of phalanges exceeds five, producing the condition called hyperdactyly.

The 5th metatarsal bone is an object of interest. Normally this bone is straight, as in the amphibia, the most primitive reptiles (Cotylosauria), the Theromorph and allied reptiles and the mammals. In other groups of reptiles, however, it is peculiar in being hook-shaped, and the possessors of this modified type of 5th metatarsal are : Sphenodon, lizards, tortoises, crocodiles, Dinosaurs, and Pterosaurs. It is worthy of note that these groups all have characters in common in the structure of the heart or of the skull, and are regarded as belonging to the great Sauropsidan branch of the reptiles which culminates in the birds. It is probable that the hook-shaped metatarsal is characteristic of this group, and distinguishes it from the other main stem of reptiles (Theropsida) which evolved in the direction of mammals. The evidence from the 5th metatarsal fits in with that obtained from other sources.

Mention must be made of those animals which have lost their limbs. They have totally disappeared in some of the eels. Among the amphibia, the pelvic limbs and girdle have been lost in the Sirenidæ, and the worm-like Gymnophiona have lost all the limbs and girdles. Coming to the reptiles, the snakes have lost the girdles and the pectoral limbs altogether, while only very small vestiges of the pelvic limbs remain. Several families of lizards have independently assumed the snake-like form by loss of the limbs, such as the slow-worm (Anguis), some of the Scincidæ and the Amphisbænidæ. These forms furnish an interesting example of convergent evolution. Among mammals the pelvic girdle and limbs vanish almost completely in the whales (Cetacea) and Sirenia.

LITERATURE

GOODRICH, E. S. Vertebrata Craniata, Cyclostomes and Fishes. Black, London, 1909.

GOODRICH, E. S.   On the Classification of the Reptilia. Proceedings of the Royal Society, Ser. B, vol. 89, 1916.
GREGORY, W. K.   Present Status of the Problem of the Origin of the Tetrapoda.   Annals of the New York Academy of Sciences, vol. 26, 1915.

WATSON, D. M. S.   The Evolution of the Tetrapod Shoulder Girdle and Forelimb.   Journal of Anatomy, vol. 52, 1917.
———.   The Evolution and Origin of the Amphibia.   Philosophical Transactions of The Royal Society, Ser. B, vol. 214, 1926.

CHAPTER XXIII

THE TAIL

AN extension of the body behind the anus, containing all the chief tissues of the body, is a structure characteristic of chordate animals. Its original function was to assist the animal in swimming, for it contains myotomes and a portion of the notochord, and so is able to take part in the undulatory movements from side to side which propel the animal forwards through the water. The area of the tail is commonly increased by the formation of a fin in the middle line, in the lower chordates. In Amphioxus, the fin is not very large, but it extends symmetrically from the middorsal and midventral lines of the tail, and tapers to a point behind. This primitive type of tail is called diphycercal. It is present also in the Cyclostomes, where it is supported by cartilaginous radials, and in early stages of development of other forms.

In Selachians the tail is asymmetrical, for the vertebral column is bent slightly dorsally, and the dorsal (epichordal) lobe of the caudal fin is reduced while the ventral (hypochordal) lobe is increased. The ventral lobe is supported by the elongated hæmal arches of the vertebral column, known as the hypurals, and not by separate radials. This type of fin is called heterocercal. In addition to the Selachii, it is present in the sturgeon, the Osteolepidoti and the fossil Dipnoi. Since the axis of the tail in such forms is bent up, in swimming, the head of the fish tends to be turned down, as when the fish noses along the bottom in search of its prey.

In the higher bony fish (Teleosts) the dorsal lobe of the caudal fin is further reduced and the ventral lobe enlarged, with the result that the tail presents an externally symmetrical

(usually forked) appearance. Internally, however, the skeleton reveals the fact that this homocercal type of tail is derived from the heterocercal, and the axis can be seen to bend up at the tip. It is found also that during development, the homocercal tail passes through a heterocercal stage.

In other forms the tail tapers symmetrically to a point, and so comes to resemble the diphycercal type. This secondarily simplified type of tail (shown by the eel, for example) is called gephyrocercal, and is the result of reduction from the heterocercal or homocercal condition. The tail-fin of Gadus is
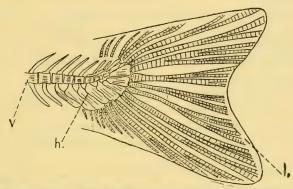
FIG. 165.—Skeleton of the tail of the salmon, showing the homocercal pattern of tail-fin characteristic of most Teleost fish.

Note the up-turned vertebral column. *h*, hypurals ; *l*, lepidotrichia ; *v*, vertebra.

peculiar, for it is formed from the hind portions of the median dorsal and ventral fins. Such a tail is called pseudocaudal.

In Ceratodus, the tail seems to be diphycercal (and therefore primitive), because its ventral lobe is supported by separate radials, and not by hypurals. There is, however, doubt about this, because many of the fossil Dipnoi had heterocercal tails, and if it can be proved that Ceratodus is descended from them, the structure of its tail must be gephyrocercal.

In amphibia, the tail-fins are present in the larval stages, which live in water ; but they disappear when the animals come out on land, to grow again in some during the water sojourn of the breeding season. In the Anura (frogs and toads)

the tail disappears altogether in the adult terrestrial form ; in the Urodeles (newts) it persists as a more or less tubular structure. In the Gymnophiona there is scarcely any tail at all, for the anus is almost at the hind extremity of the animal. In land-animals, the tail ceases to have the function which it exercised in the water, and it is often consequently much reduced. Instead of being a posterior prolongation of the body, it has the appearance of being merely an appendage, and it is of use to the animal in the maintenance of its balance, as a covering for the anus and genitalia, and in some cases as a fly-whisk.

Lizards have an interesting modification in that the vertebræ of the tail are cleft transversely, and it is at these points that the tail can be detached from the rest of the body. This faculty (autotomy) is of service to the animal in enabling it to escape from its enemies.

The primitive birds had long tails, with separate vertebræ, as is shown by Archæopteryx. In living birds the caudal vertebræ are fused together to form the pygostyle, and the tail itself is much reduced. The so-called tail of birds consists of the tail-feathers.

In some arboreal animals, such as the chamæleon and the American monkeys, the tail is prehensile and capable of grasping objects.

It is common to find that in those vertebrates which have returned to the water, the tail is well developed and expanded into fins. While superficially not unlike the tails and caudal fins of fish, they show in their structure fundamental differences. So in Ichthyosaurus, the vertebral column passes back into the ventral lobe of the fin ; in the whales the two lobes of the caudal fin are not dorsal and ventral but right and left, for the tail is expanded horizontally.

In the apes and man the external tail has disappeared altogether.

CHAPTER XXIV

THE VASCULAR SYSTEM

THE vascular system is remarkably uniform in its main features in all chordates. It consists essentially of four longitudinal vessels running along the whole length of the animal. Of these, one runs under the gut in the gut-wall (subintestinal vessel) ; the other three run in the body-wall, and are the dorsal aorta and the paired cardinal veins respectively. The subintestinal vessel connects with the dorsal aorta at the anterior end of the animal by a number of paired vessels which run up round the gut on each side passing in between the gill-slits. The anterior prolongations of the dorsal aorta (which is paired in the anterior region) are the internal carotids. Farther back the dorsal aorta gives off small vessels in each septum (between the segments) to the tissues of the body-wall, and other vessels which pass down the mesentery supporting the gut to supply the gut-wall. The blood in the gut-wall is collected up into the subintestinal vessel and is led forwards again. On the way, it breaks up into capillaries again in a glandular diverticulum of the gut—the liver, and deposits much of the digested and absorbed material which it has picked up in the posterior region of the gut (intestine). In this way a hepatic portal system is formed. The blood in the body-wall makes its way to the cardinal veins, and from them it crosses the cœlomic cavity between the body-wall and the gut-wall by the ductus Cuvieri (or superior vena cava), running in the transverse septum, to the subintestinal vein. This is the fundamental type on which the peripheral vessels are arranged in all chordates, and the details in the various groups can be considered under the headings, veins, heart,
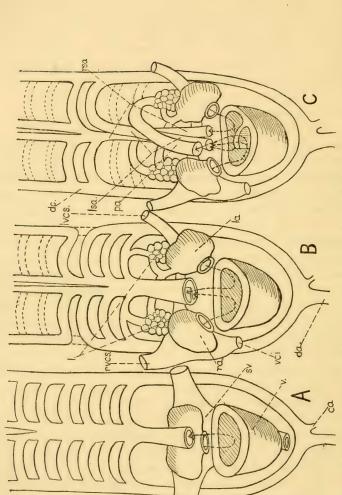
Fig. 166a.—Diagrammatic representation of the heart and aortic arches of A, a fish ; B, an amphibian ; C, a lizard.
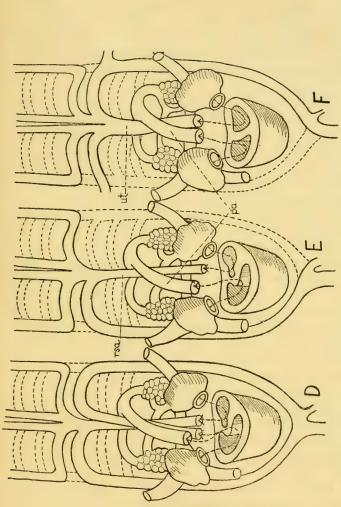
Fig. 166b.—Diagrammatic representation of the heart and aortic arches of D, a crocodile; E, a bird; and F, a mammal.

The heart is represented as cut across, so that the observer is looking from the ventral side back into the ventricle, and forwards into the auricles and the bases of the truncus and arterial arches. *ca*, cœliac artery; *da*, dorsal aorta; *dc*, ductus caroticus; *l*, lung; *la*, left auricle; *lsa*, left systemic arch; *lvcs*, left superior vena cava; *pa*, pulmonary arch; *ra*, right auricle; *rsa*, right systemic arch; *rvcs*, right superior vena cava; *sv*, sinus venosus; *ut*, undivided systemic trunk; *v*, ventricle; *vci*, inferior vena cava.

and arteries. It may be remembered that arteries are vessels leading blood away from the heart, and veins lead blood towards the heart, whatever be the kind of blood which they contain. Further, arterial blood is rich in oxygen, and venous blood poor in oxygen, whatever may be the nature of the vessel which contains it. Actually, the purest arterial blood in the body is in a vein (pulmonary), and the foulest venous blood is in an artery (also pulmonary).

The Veins.—The description given above applies to the venous system of Amphioxus. In the Craniates, the presence of mesodermal kidneys (pronephros and mesonephros), lying in the track of the posterior cardinal veins, brings about the formation of a renal portal system. The anterior cardinal veins give rise to the jugulars, and in the Gnathostomes there are veins returning blood from the fins or limbs. Those from the anterior limbs are the subclavian veins which run into the ductus Cuvieri; those from the hind limbs are the pelvic veins which run into the renal portals and into the lateral abdominal veins. The two latter veins often join in the middle line on the ventral side and give rise to the anterior abdominal vein of Ceratodus and higher forms. In the amniotes the lateral abdominal veins receive the blood from the allantois in the embryonic stages of development. Beginning in the Dipnoi, there is another connexion between the circulation of the body-wall and that of the gut-wall, apart from the superior venæ cavæ. This is the inferior vena cava. Pulmonary veins are present in Polypterus, Dipnoi, and Tetrapods, returning blood from the lungs to the heart. In the amniotes the renal portal veins tend to diminish owing to the fact that the functional kidney of the adult is no longer a mesonephros but a metanephros, and in the birds and mammals there is no renal portal system.

The Heart.—In Amphioxus there is no specialised heart in which the blood is pumped forwards, but, apart from the specialised bulbils, the whole vascular system is contractile and propels the blood along. Beginning in the Cyclostomes, there is a definite portion of the subintestinal vein in front of the liver and behind the gill-slits which is set apart as a muscular

pump, and forms the heart. The veins from the liver and the ductus Cuvieri are received by a sinus venosus, which in turn leads into a thin-walled auricle. The latter passes the blood on to the thick-walled muscular ventricle, by which it is propelled into the anterior portion of the subintestinal vessel which is called the ventral aorta. The arteries are surrounded by smooth muscle, but the musculature of the heart is peculiar and unique in that it shows a number of cross-striations and its fibres branch. The openings between the various subdivisions of the heart are guarded by valves which prevent a return flow.

In Scyllium the ventricle is produced forwards into a muscular and contractile conus, which contains several rows of valves. In front of this, the base of the ventral aorta is swollen into a non-contractile bulbus. (The walls of the conus contain heart-muscle, those of the bulbus smooth muscle.) In the higher bony fish the conus tends to disappear while the bulbus enlarges. Amia is primitive in showing a fairly large conus with three rows of valves. In the Dipnoi, the valves of the conus are well developed, and they give rise to a spiral septum which almost or quite divides the conus into two. These same forms are further very interesting in that the ventral aorta is very much shortened up into a truncus (instead of extending forwards all the way beneath the gills as in Scyllium), and also because in Ceratodus there is a beginning of the subdivision of the auricle into two, with the pulmonary veins running into the left subdivision.

In the frog, the heart is not unlike that of Ceratodus, except that the auricles are completely divided into two, and that the spiral septum in the conus and truncus is better developed, dividing a pulmonary channel (leading to the pulmonary arches) from an aortic channel (leading to the aortic and carotid arches).

In the water-breathing forms, the heart is always full of venous deoxygenated blood, while in air-breathing forms there is always a double stream of blood in the heart. One of these streams is arterial and oxygenated, and the other venous and deoxygenated. Since in the frog there is only one ventricle,

and both the arterial blood from the left auricle and the venous blood from the right auricle open into it, there is a mixture in the ventricle which is sorted out into the two channels in the truncus by the spiral septum and valves. In newts, the septum between the auricles tends to break down, as does the septum in the truncus. In the embryonic stages of amniotes the septum between the auricles remains incomplete also, until the time of hatching or birth, in connexion with functional details of the embryonic circulation.

The hearts in the amniotes fall into two classes, neither of which can be derived from the other, and which must have been separately evolved from the amphibian condition. The conus is reduced and incorporated in the wall of the ventricle, but while in one group which may be called Sauropsidan the truncus is split right down to the ventricle into three channels, in the other or Theropsidan group it is split into only two channels.

The three channels in the Sauropsida are the pulmonary, the right systemic, and the left systemic. The two latter cross over one another so that the right systemic springs from the left side of the ventricle, while the left systemic arises with the pulmonary from the right side of the ventricle. In the lizards, snakes, tortoises, and Sphenodon, the ventricle is still single, although there is a septum which divides it incompletely. The left auricle, as always, contains the arterial blood, most of which goes into the right systemic arch. In the crocodile, the interventricular septum is complete, but it is formed in such a way that while the right systemic arch gets all the arterial blood from the left auricle, the left systemic arch together with the pulmonary, gets only venous blood from the right auricle. There is a small foramen (of Panizza) between the right and left systemic arches which allows a little interchange of blood. The condition in the bird is like that of the crocodile except that the left systemic arch has been abolished altogether, which is not surprising, seeing that it could only distribute blood which is almost purely venous. In the bird, therefore, with its four-chambered heart, there is no mixture of arterial with venous blood ; all the venous blood in the

heart goes to the lungs and only to the lungs. In reptiles and birds, the carotids arise from the right systemic arch.

The two channels of the truncus in the Theropsida are the pulmonary and the single systemic aorta. These forms include the mammals, and the Theromorph reptiles, although the latter (fossils) are obviously only known from their skeleton. The heart is four-chambered, and the ventricle is completely divided into two, so that all the venous blood from the right auricle goes into the pulmonary arch, and all the arterial blood from the left auricle into the systemic aorta, and there is no mixture. It so happens that the aortic arch of the right side does not persist, and only the left one remains, but it is of the utmost importance to realise that the reason why there is a single systemic arch in the bird is totally different from that which is responsible for the single arch in the mammal. The structure of the heart in the amniotes shows that the reptiles contain two main lines of evolution (besides other less important lines), the one culminating in the birds and the other in the mammals. The sinus venosus disappears in the highest forms, birds and mammals, and is represented by the so-called sino-auricular node. This structure is of great functional importance, for it acts as the pace-maker to the heart. It is here that the contraction originates, which contraction then becomes taken up by the other parts of the heart, and constitutes its " beat." In birds and mammals the superior and inferior caval veins open direct into the right auricle. The sino-auricular valves give rise in the mammals to the Eustachian and Thebesian valves.

The Arteries.—In the fish typically, each of the visceral arches has an afferent branchial artery leading from the ventral aorta to the gills, and an efferent branchial artery connecting the gills to the lateral dorsal aorta. The vessels in the mandibular arch become reduced. The general arrangement of these vessels is necessitated by the presence of the visceral clefts, which make it impossible for the vessels to reach the dorsal side of the gut from the ventral side except by passing in the visceral arches between the clefts. Since gill-slits or pouches are present in the embryos of all chordates, the same

reason accounts for the arrangement of the arterial arches in the higher forms. In the air-breathing vertebrates, the gills are reduced and there is a continuous vessel in each visceral arch running from the truncus arteriosus (ventral aorta) to the lateral dorsal aorta. In Salamandra all the vessels in the 3rd to 6th visceral arches persist. The 3rd becomes the carotid, the 4th and 5th become systemics, and the 6th is the pulmonary. All these arterial arches place the truncus in communication with the lateral dorsal aorta. The lateral dorsal aortæ are, however, interrupted between the dorsal ends of the 3rd and the 4th arterial arches; *i.e.* there is no ductus caroticus. The conditions in Triton are similar except that the 5th arterial arch has completely disappeared. In Lacerta (as in all higher forms) the 3rd arch persists as the carotid, the 4th as the systemic, and the 6th as the pulmonary. In Lacerta, the connexion between the dorsal ends of the arteries of the 3rd and 4th arches persists, forming the ductus caroticus. The lateral dorsal aorta is here accordingly uninterrupted. The ductus caroticus is absent in the adult of higher forms. The connexion between the pulmonary arch and the lateral dorsal aorta is the ductus arteriosus. This connexion is important in the embryonic stages of Amniotes. It enables the blood from the right side of the ventricle (or the right ventricle, if it is separated off) to reach the lateral dorsal aorta through the pulmonary arteries, instead of going to the lungs. At these early stages of development the lungs are not yet open. In the adult amniote, the ductus arteriosus usually degenerates into a ligament, as, for example, in the mammal (on the left side), or disappears. It persists, however, in some turtles, and their case is interesting, for they are in the habit of diving, and during the submerged period the lungs are not working. The blood in the pulmonary artery can then escape into the general circulation without going through the lungs. The ductus arteriosus is also called the ductus Botalli.

In the frog, there is neither ductus caroticus nor ductus arteriosus in the adult.

In the Sauropsidan reptiles, the right and left systemic arteries of the 4th arch are separate right down to the base of

the truncus. The left one of these arches is absent in the bird. The subclavian arteries come off from the right systemic arch in lizards (dorsal type of subclavian) ; in Chelonia, crocodiles, and birds, the subclavian arteries are given off from the carotids (ventral type).

In the mammal, the right and left arteries of the 4th (systemic) arch differ from those of the Sauropsidan reptiles in that the aorta is undivided, instead of being split to its base. The artery on the right side does not reach round to the dorsal aorta ; it is given the name of innominate artery, and it leads to the right carotid and subclavian arteries. That on the left side forms the so-called aorta, gives off the left carotid and subclavian arteries, and continues back as the dorsal aorta. It is connected with the pulmonary arch by the ductus arteriosus as already mentioned.

The internal carotid arteries are the anterior prolongations of the lateral dorsal aortæ, and they enter the skull by passing up between the trabeculæ, close to the pituitary body. The external carotids are the anterior prolongations of the ventral aorta, on each side of the thyroid.

The proximal ends of the arteries and veins are joined at the heart. The distal ends of the arteries are connected with those of the veins by the capillaries, so that the whole vascular system is a closed one. When a vein starts from capillaries and breaks down into other capillaries again before reaching the heart, it is known as a portal vein. The hepatic portal vein occurs in all chordates, the renal portal appears in the Cyclostomes and disappears in the amniotes.

The blood of Amphioxus is colourless, but in all higher forms, hæmoglobin, a respiratory pigment, is present in corpuscles, which become known as " red blood-corpuscles." In the adult mammal, these corpuscles are peculiar in being non-nucleated. The white corpuscles of the blood play an important part in the defence of the organism against invasion by foreign bodies. In the embryo, the blood arises from blood-islands, between the mesoderm and the endoderm in the region of the yolk. In the adult, blood-corpuscles are formed in the marrow of the bones, and in the lymphatic organs. The

blood is under pressure in the arteries and capillaries, owing to the contraction of the smooth muscle surrounding the former and of the Rouget-cells which compose the walls of the latter.

Lymphatics.—Attention may now be turned to the lymphatic system. In addition to the blood-vessels, the body contains a system of vessels, channels, and spaces in which lymph circulates, forming the lymphatic system. It is in communication with the cœlomic cavity. Lymph is blood-plasma and white corpuscles which exude from the capillaries and bathe all the tissues of the body, supplying them with nutritive products. From the tissues, the lymph (which may thus be regarded as blood minus the red blood-corpuscles) is gathered up into thin-walled channels, called the lymphatics. These start from blind ends and eventually join the veins, in particular the subclavians, the left of which receives the main lymphatic trunk which is known as the thoracic duct. In the amphibia the space between the skin and the muscles of the body-wall is occupied by lymph, and in certain regions "lymph-hearts" are present, with muscular walls, which propel the lymph along. These lymph-hearts are lacking in mammals. Lymphatic vessels are present in the wall of the intestine, and are known as lacteals, for they absorb the fatty products of digestion, and the milk-like emulsion which they contain gives them a white appearance. Here and there along the lymphatics, lymph glands are formed. To these belong the spleen (which first appears in the Selachii), the tonsils (derived from the 2nd pair of visceral pouches), and Peyer's patches along the intestine in the mammals.

LITERATURE

GOODRICH, E. S.   Vertebrata Craniata, Cyclostomes and Fishes.   Black, London, 1909.

GOODRICH, E. S.   On the Classification of the Reptilia.   Proceedings of the Royal Society, Ser. B, vol. 89.   1916.

CHAPTER XXV

THE RESPIRATORY SYSTEM

ALL chordates have a closed vascular system and hæmoglobin as a convenient transporter of oxygen. Their respiratory systems involve structures in which blood-vessels are brought into close contact with the surrounding medium (water or air) with as little intervening tissue and as great an exposed surface as possible. The former requirement is met by the very thin nature of the epithelium covering the blood-vessels, and the latter by reducing the size of the blood-vessels to capillaries, which therefore have a large surface compared with their volume.

The respiration of embryos within their membranes is effected by various means, such as the circulation of the yolk-sac or of the allantois, as has been described in connexion with the development of the frog, chick, and rabbit.

After the embryonic stage has been passed, chordates breathe either by gills, or by gills and lungs (sometimes assisted by the skin), or by lungs alone.

Gills are groups of capillaries in the walls of the gill-slits, through which water passes out from the pharynx. In Amphioxus the current of water is caused by the action of the cilia on the under side of the oral hood and in the gill-slits themselves. Fish breathe in the following manner : the gill-slits are shut and the floor of the mouth is lowered, which causes water to enter the mouth. The mouth is then closed, its floor is raised, and the water escapes through the gill-slits. When Cyclostomes are feeding, they are firmly attached to their prey by their mouth and the sucker surrounding it. They cannot therefore take in water through the mouth, and

the gill-pouches are modified into sacs which pump water in and out again. In the larvæ of some fish (Polypterus, Lepidosiren), and in those of amphibia, external gills may be developed in the form of tuft-like structures projecting out from the body into the water, and which enable the blood to be oxygenated before the gill-slits are pierced. The larval amphibia afterwards develop ordinary gills on the outer faces of the gill-arches, and their respiration is like that of the fish. In all these cases the respiratory movements are brought about by means of the contraction of visceral muscles, innervated by dorsal cranial nerve-roots, and controlled by a centre in the medulla oblongata.

The first visceral cleft or spiracle is open in the Selachii, but it is closed in all higher forms with the exception of Polypterus and Acipenser (the sturgeon). There may be a spiracular gill, which is called a pseudobranch because its capillaries receive blood which has already been oxygenated in the next posterior (true) gill. In the Tetrapods the cavity of the spiracular cleft gives rise to the tympanic cavity and Eustachian tube.

The rays are Selachii adapted for living on the sea-bottom, and they are of a flattened shape, with the gill-slits on the under side. The spiracle is on the upper side, and serves to admit water into the pharynx. In the Selachii, the gill-slits are uncovered, but in the bony fish (Dipnoi and Teleostomes) they are covered over and protected by an operculum. An analogous operculum develops in the larva of the frog, and it may be remembered that in Amphioxus the gill-slits are protected by being enclosed in the atrial cavity.

The gill-sacs of Petromyzon all open independently to the exterior, whereas those of Myxine have a single joint opening on each side.

The number of gill-slits in Amphioxus is large (up to 180). In Selachii, not counting the spiracle, it is five, except in Heptanchus which has seven, and Hexanchus and Pliotrema which have six. Five is also the number in bony fish. It is important to remember that gill-slits or pouches are present in early stages of development of all chordates up to and

including mammals, and that they play a part in the disposition of the arterial arches although they cease to function as respiratory organs.

The adult Amphibia (or most of them, *i.e.* those which have not lost the lungs) and all higher vertebrates breathe by lungs. (The use of the skin as a breathing organ in Amphibia is made possible by the fact that their skin is moist and uncovered.)

Lungs are also present in some fish. In Polypterus, there is a trachea leading out from the ventral side of the œsophagus, and forking into two lungs. The cavity of these lungs is divided into small spaces or " cells," which has the result of increasing the internal surface. Such lungs are called cellular, and they are supplied with blood by pulmonary arteries, *i.e.* branches from the last (6th) pair of branchial arterial arches. From them, blood returns (to near the sinus venosus) by paired pulmonary veins. In the Dipnoi, there are paired lungs in Protopterus and Lepidosiren, but a single one only in Ceratodus. Their relations are similar to those of Polypterus, except that the lungs, together with the pulmonary arteries and veins, have been displaced to a dorsal position by passing round the right side of the œsophagus. In Ceratodus the pulmonary veins open into the left side of the auricle. Lungs were almost certainly present in the Osteolepidoti. These animals lived or live in fresh water in which the oxygen-content is low (owing to desiccation and accumulation of decomposing organic debris), and branchial respiration is supplemented by the intake of bubbles of air through the mouth. Indeed, Protopterus is able to withstand periods of drought when the swamps in which it lives dry up, by burying itself in the mud and breathing by its lungs. The lungs of higher vertebrates are easily derived from those of the fish just described. It is possible that the lungs respresent a pair of gill-pouches behind the remainder, and which ceased to open to the exterior. They are formed from the endoderm and communicate with the alimentary canal, and they preserve their blood-supply from the vessel of the last branchial arch.

In the higher bony fish, the lung is single and modified.

In the primitive form Amia, it is still supplied with blood from the last branchial artery and its walls are cellular, but in all the rest it derives blood from the cœliac artery and dorsal aorta, and its walls are not adapted for the diffusion of gases through them, except in a restricted vascular area. In some forms it remains connected with the alimentary canal by an open tube, but in others it is completely shut off (in the adult condition). In these higher bony fish, the lung no longer functions as a respiratory organ, but it has become a hydrostatic organ. The quantity of gas which it contains is regulated by the vascular area just referred to (where oxygen may be passed from the blood into it or vice versa), and the fish is able to adapt its specific gravity to that of the depth of the water at which it is swimming. It is therefore able to maintain its depth without muscular effort. In these forms it is no longer a lung, but an air-bladder or swim-bladder. In some Teleosts, such as the catfish (Amiurus), the swim-bladder enters into relations with the auditory vesicle, and is connected with it by a chain of small bones called the Weberian ossicles, which are derived from the first three vertebræ. In some other Teleosts, the swim-bladder disappears in the adult, and these are often found to be bottom-living forms, which live at a more or less constant depth.

Strange as it may seem, therefore, it is probable that the lungs were evolved while the vertebrates were still in the water, and that they gave rise to the swim-bladder by specialisation.

It is now necessary to turn to the relations which the olfactory organs bear to the respiratory system. In the Selachii and the higher bony fish, the nasal sacs have no connexion with the mouth, but this is not the case in the most primitive bony fish. In Osteolepis and in the Dipnoi there are external nostrils on the snout, and they lead to internal nostrils which open into the mouth-cavity. This condition is also present in all the Tetrapods. In these forms, therefore, the olfactory organs are subservient to the respiratory system in that they enable the respiratory medium (water or air) to enter the mouth-cavity without having to pass through the

mouth itself. It may be remembered that in Petromyzon the nostril is single and confluent with the opening of the hypophysial sac. The same is true of Myxine, but here the hypophysial sac opens into the alimentary canal. This connexion between nose and gut is, however, quite different from that of the other forms just mentioned, and was independently acquired.

The amphibia when adult breathe air into their lungs, but the mechanism for doing so is similar to that which the fish use for breathing with their gills. The floor of the mouth is lowered and air is taken into the mouth cavity. The mouth and nostrils are then closed, and the floor of the mouth raised, which forces the air down the throat and larynx into the lungs.

The method of respiration in the amniotes is more efficient. The volume of the lungs is increased by the expansion of the thoracic box, and this is accomplished by movements of the ribs (assisted in the mammals by movements of the diaphragm). The muscles concerned in these movements are somatic and innervated by ventral nerve-roots of the neck and thorax. The tortoises, whose ribs are, of course, fixed to the carapace which surrounds them, replenish the air in their lungs by movements of the neck, arms, and legs.

The lungs of Polypterus, Dipnoi, and amphibia are more or less hollow sacs. In reptiles the internal surface of the lungs are increased by foldings of the walls, with the result that the lungs can no longer be described as simple hollow sacs. In birds and mammals, this process has been carried still further, and the lungs are spongy masses of tissue penetrated by innumerable small air-spaces. In mammals, the internal surface-area of the lungs may be thirty times that of the external surface of the body.

The lungs of the chamæleon are of interest in that they are produced into a number of blind diverticula or air-sacs. These air-sacs reach their highest degree of development in the birds, in which they may occupy a large volume. Air is led into the air-sacs from the bronchi passing straight through the lungs, and it then passes back into the lungs where it oxygenates the blood, and out again through the trachea. The

efficiency of this mechanism lies in the fact that there is a through-draught right through the lungs. All the air can be renewed, whereas in other forms, the lungs are blind sacs and there is always a certain amount of stale residual air at the bottom of them which cannot be renewed. The efficiency of the respiratory system has played a large part in the evolution of the birds, which require a high rate of metabolism in order to perform the very arduous muscular exertion of maintaining the body in the air during flight.

Attention may now be turned to two modifications which may occur in connexion with the respiratory system. The first concerns the formation of the false palate. This structure is a secondary roof to the mouth, closing over the original internal nostrils, and enclosing the nasal passage as far back as the secondary choana. The secondary choana is opposite the glottis (the opening through which the pharynx communicates with the larynx and trachea, and so with the lungs), and the whole structure is an adaptation enabling the animal to breathe and yet have its mouth full of food or water at the same time. It is especially developed in aquatic forms such as the crocodile and the whale, but it is characteristic of the higher Theromorph reptiles and mammals in general. In the whales the glottis can be pushed right up into the secondary choana, thus making a closed communication between the external nostrils (above the surface of the water) and the lungs, without running the risk of water entering the latter from the mouth. In the higher vertebrates, and especially those which frequent deep waters, the windpipe or trachea is prevented from collapsing by rings of cartilage or bone.

The fact that respiration in terrestrial vertebrates involves the pumping of air in and out of the body, has been made use of in connexion with the production of sound. Bands of connective tissue stretch across the cavity of the larynx, and can be thrown into vibration by the passage of the air. These bands are the vocal cords. In the male frog there are vocal sacs at the corners of the mouth, and these become distended with air when the animal " croaks " and act as resonators.

The larynx and its vocal cords are the organ of voice-production in the mammal, and the pitch of the sounds can be controlled by the tension of the cords and the laryngeal muscles. The false palate acts as a resonator. In the birds there is a special organ called the syrinx situated at the fork where the trachea divides into the two bronchi, and it is to the vibrations of this that the song of birds is due.

It is interesting to note that the power of producing vocal sounds has evolved parallel with the capacity for appreciating them, or in other words, the differentiation of the cochlear part of the ear.

LITERATURE

GOODRICH, E. S. Vertebrata Craniata. Cyclostomes and Fishes. Black, London, 1909.

OPPEL, A. Atmungsapparat : Lehrbuch der Vergleichenden Mikroskopischen Anatomie der Wirbeltiere. Part 6. Fischer, Jena, 1905.

CHAPTER XXVI

THE ALIMENTARY SYSTEM

THE alimentary system comprises the tube which leads from mouth to anus, together with the glands attached to it which aid in the processes of digestion. There is a slight invagination of the ectoderm at the mouth and anus, forming the stomodæum and the proctodæum; but the remainder, which forms by far the larger part of the alimentary system, is formed exclusively from the endoderm. In addition to the digestive glands, the alimentary canal has a number of derivatives which have been considered in connexion with other organ-systems. So the gill-pouches and the larynx and lungs belong to the respiratory system; the allantoic bladder forms part of the excretory system; while the thyroid gland, which in Gnathostomes and adult Cyclostomes is one of the endocrine organs, belongs to the alimentary system in Amphioxus and the larval Cyclostome (Ammocœte).

The primitive method of obtaining food is by the creation of a current of water towards the mouth by means of cilia. This is the case in Amphioxus (and the Ascidians). Here the endostyle is accessory to the alimentary system in that it ensures that the particles of food reach the intestine instead of being lost with the current of water flowing out through the gill-slits. The method of feeding by means of a sucking mouth and a rasping tongue which is characteristic of the Cyclostomes, is secondary and specialised. In all the Gnathostomes, the most anterior visceral arches, between the mouth and the first visceral cleft, become modified and adapted for seizing food, and give rise to the jaws. This method enables food of larger size to be obtained than is possible by the ciliary

method, and the Gnathostomes were thereby able to evolve to greater size. In these forms also, the jaws are garnished with teeth, and the nature and shape of the teeth varies with the kind of diet. Not only do teeth assist in seizing prey, but in the higher forms they serve to grind it up small, which is an aid to the processes of digestion. In the higher vertebrates, the tongue may also be used for obtaining food as in the case of the chamæleon, and it assists in the process of swallowing.

In the primitive forms the alimentary canal or gut runs straight from mouth to anus, as in Amphioxus and the Cyclostomes. In these two forms the lining of the gut is ciliated, but in higher forms the ciliation is restricted to certain anterior regions. Food is propelled along by peristaltic action of the smooth muscle in the gut-wall.

Beginning in the Selachians, a special part of the gut is modified as a receptacle in which food is treated with digestive juices secreted by its walls, and in which absorption does not take place. This is the stomach, and in all Gnathostomes it is an enlarged region of the gut, kinked to the left side of the body, and situated between the non-digestive supply-tube or œsophagus and the absorbent intestine. The intestine of the Gnathostomes is greater in length than the space which contains it, with the result that it is more or less coiled. In the higher forms the intestine is very considerably longer than the body itself. The effect of this is to increase the surface of absorption. A modification which serves the same function is the spiral valve in the intestine, which is feebly developed in Petromyzon and well developed in the Selachians. The spiral valve is also present in Ceratodus and in a few primitive bony fish (Teleostomes), but it is lost in all higher forms. A peculiarity of the stomach of the higher bony fish (Teleostei) is the development of a number of blind outgrowths (pyloric cœca) from the hinder end of the stomach. The wall of the intestine is well supplied with blood-vessels belonging to the hepatic portal system, and with lymphatic vessels or " lacteals."

The œsophagus in birds is modified and enlarged into a crop or temporary storage place. The stomach is divided

into two regions. The first of these, the proventriculus, has soft walls provided with glands. Next comes a hard-walled gizzard, in which the food is crushed with the help of stones, for the bird has no teeth and so cannot perform this function in the mouth.

In mammals, the stomach is simple except in a group of the Ungulates called the Ruminants, where it is divided into several parts. These animals " chew the cud," and their stomach is modified in consequence. The food (grass) is swallowed down (without being masticated) into the anterior divisions of the stomach composed of the paunch and the " honey-comb." When the animal ceases feeding, the food is brought up to the mouth again and thoroughly chewed and salivated. It then redescends to the other divisions of the stomach, termed the maniplies and the abomasum. The latter has glandular walls, and secretes digestive juice.

The region between the intestine and the anus is short and straight in the lower forms, and is called the rectum. It is usually marked off from the intestine by the development of a constriction, the ileo-colic sphincter, and by one or two blind diverticula or cœca. In the Tetrapods the region between the intestine and the anus becomes longer and coiled, and it becomes possible to distinguish a so-called large intestine (on account of its diameter) or colon which is coiled, from the terminal straight rectum. The intestine proper is then called the small intestine. The large intestine is concerned with the absorption of water from the non-digested remains of the food, a function of importance for animals which inhabit dry land.

The cœcum in mammals may be very large, as in the rabbit, and this condition is common in herbivorous animals. The cœcum contains a colony of bacteria whose function it is to attack the cellulose of the food and to digest it. In other forms the cœcum is reduced, and may be represented only by its tip, the vermiform appendix, as in man.

The anus primitively opens to the outside in conjunction with the urino-genital ducts, forming a cloaca. This condition is departed from in the higher bony fish (Teleostomes) and in the higher mammals or Ditremata (Marsupials and

Placentals), in which the alimentary and urino-genital systems open separately to the exterior.

The first special digestive gland to appear is the liver, which is present in Amphioxus. In the higher forms it connects with the anterior part of the intestine by the bile-duct, and usually possesses a gall-bladder. A rudimentary pancreas appears in the Cyclostomes, and in higher forms it is well developed, connecting with the intestine by one or more pancreatic ducts. It may be mentioned that in mammals at least, the secretion of pancreatic juice is started by a substance " secretin," which is released from the lining of the intestine into the blood-stream and carried therein to the pancreas which it stimulates. This is of interest, for secretin was the first of the hormones (chemical stimulants with specific effects and which are carried about in the blood) to be properly recognised.

Salivary glands are lacking from the lower water-living chordata, as is readily understood when it is remembered that a current of water is constantly sweeping through the mouth to the gill-slits. Salivary glands make their appearance in the Amphibia. In the snakes, some of the salivary glands may be modified into poison-glands.

LITERATURE

OPPEL, A. Der Magen, Schlund und Darm, Mundhöhle, Bauchspeichel-drüse und Leber. Lehrbuch der Vergleichenden mikroskopischen Anatomie der Wirbeltiere, Parts 1, 2, and 3. Fischer, Jena, 1896.

CHAPTER XXVII

AMPHIOXUS is unique among chordate animals in possessing true nephridia. These organs are situated above the gill-slits, their solenocytes project into the lateral dorsal cœlomic cavities, and their external openings lead into the atrial cavity. The gonads of Amphioxus are segmental, and situated at the ventral ends of the original myocœlic cavities. The germ-cells of each segment make their way independently to the exterior (actually into the atrial cavity) by pores in the body-wall.

It is possible that the region of the cœlom, which in all higher Chordates is concerned with the formation of the excretory organs, corresponds to that region which in Amphioxus forms the gonads.

Originally there must have been a continuous row of little tubes on each side of the body, leading out of the splanchnocœl into a duct which collected from them all, and opened to the outside at or near the anus. These little tubes represent the original connexion between the myocœl and the splanchnocœl (the nephrocœl, in the intermediate cell-mass), and consequently they are segmental in arrangement : one tubule on each side to each segment. Such an arrangement has been called an archinephros, and the duct the archinephric duct, and this condition is almost fulfilled in the Cyclostome Bdellostoma. Here a continuous row of tubules is formed, but an intermediate section of them disappears, thus separating an anterior batch—the pronephros—from a more posterior set—the mesonephros. In other forms the pronephros appears first, and the duct which is formed by the backward growth of the ends of the tubules is the pronephric duct. The pronephros

is the functional larval kidney in the lower vertebrates, and the pronephric duct grows back to the cloaca without waiting for the mesonephric tubules to develop. When these form, they find the pronephric duct ready-made to receive them. After receiving the mesonephric tubules the pronephric duct becomes known as the mesonephric duct, and the pronephros degenerates (except in the bony fish Fierasfer and Gobiesox). The functional kidney in the adult fish or amphibian is the mesonephros.

The cavity of each tubule (pronephric or mesonephric) becomes shut off from the splanchnocœl, although the opening of the tubule into the splanchnocœl (the ciliated funnel or cœlomostome) may persist (as in Selachians and amphibia) on the median side of the occlusion. The cavity of the tubule now becomes known as a Bowman's capsule, and its wall is indented by capillaries from the dorsal aorta and leading to the posterior cardinal vein, forming the glomerulus. Bowman's capsule and the glomerulus together form a Malpighian corpuscle. Primitively, these corpuscles are segmentally arranged, and this condition is retained in Myxine. In other forms the number of Malpighian corpuscles is greatly increased by the formation of others by budding.

In the Cyclostomes, the germ-cells in the two sexes are shed into the cœlomic cavity, and make their way to the exterior by a pair of pores at the base of the mesonephric ducts. In all higher forms the sperms are never shed into the cœlom, but led by vasa efferentia to the vas deferens, primitively passing through the tubules of the mesonephros. The vasa efferentia are the cœlomic funnels leading into the tubules, and the mesonephric duct forms the vas deferens or Wolffian duct. In addition, on each side there is another duct, in the embryo. This is the Müllerian duct or oviduct, which develops in the females but becomes reduced in the males. The Müllerian duct in the Selachians arises by splitting off from the Wolffian duct, but in other forms it grows back independently from its opening into the cœlom (the oviducal funnel or Fallopian tube) in front, to the cloaca behind. The eggs then are shed into the cœlom whence they enter the oviducts,

whereas the sperms pass down a duct which serves for them as well as for the evacuation of urine from the kidney. Thus, while the Cyclostome has a single kidney-duct on each side in both sexes, and the germ-cells do not pass through it, in the fish and amphibia typically the females have two ducts on each side. One of these is the Wolffian duct evacuating the urine, the other is the Müllerian duct leading out the eggs. In the males of fish and amphibia the Wolffian duct evacuates both urine and sperms ; the Müllerian duct is reduced, and in the Selachian is represented only by the funnel and the sperm-sacs. This condition is typically represented in the frog and newt.

In several different groups of fish and amphibia, this arrangement is slightly altered by the separation of a part of the Wolffian duct conveying the sperms (vas deferens) from another part which drains the kidney (mesonephric ureter, not a true ureter). By this means, the sperms avoid going through the excretory part of the kidney, and this condition is found in the Dipnoan Protopterus, Polypterus, the Teleosts, and in such toads as Alytes, in all of which it has been independently developed. In Scyllium, it will be remembered that only the hinder part of the mesonephros is excretory in function, and the sperms pass through the anterior part.

In Lepidosteus and many Teleosts, the cœlomic wall surrounds the ovary forming a sac which joins on to the oviduct. In this manner the ovary is completely shut off from the cœlomic cavity, and consequently the eggs are not shed into it, but led directly to the exterior.

In the amniotes, the functional kidney in the adult is the metanephros, and the metanephric duct or ureter is an outgrowth from the Wolffian duct. The Wolffian duct is therefore spared the function of evacuating urine, and it persists only in the male, where it functions solely as a vas deferens for the sperm. The mesonephric tubules form the epididymis. The Müllerian duct disappears in the male, and the Wolffian duct disappears in the female. The Müllerian duct persists in the female as the oviduct. In the adult bird, only the left ovary and oviduct persist.

Except in the Monotremes, the base of the oviduct in the mammals becomes specialised to form the uterus, in which the embryos undergo development. According as to whether the bases of the two oviducts remain separate or become fused together the uterus may be double or single.

Another peculiarity of the mammalian reproductive system, is the fact that in the male, the testes usually leave their position in the roof of the abdominal cavity, and descend into scrotal sacs (see p. 150).

While claspers or copulatory organs are present in the males of several fish, the amphibia lack them (except the Gymnophiona), and fertilisation has to take place in water since the sperm require a fluid medium. In Anura the eggs and sperm are shed together into the water. In the newts, as a rule, the male lays a packet of sperm, and then gives a display of " courtship " in front of the female to stimulate her to pick up the packet with her pelvic limbs and place it in her cloaca. During the breeding season the male has specially developed secondary sexual (epigamic) characters, such as the crest and the colour of the belly, which assist in the courtship activities.

In the amniotes, fertilisation is internal, and the sperms are introduced into the cloaca of the female by the copulatory organ or penis of the male. In this way, the amniotes are independent of water for fertilisation.

A feature of considerable interest is the increase in care of the young after they are hatched, by the parents. This increases in the higher groups of vertebrates, and all stages can be found in the evolution of the family, from the condition of Amphioxus where fertilisation takes place in the sea water outside the parents which are in no way concerned with the development of the young, to that of man. This evolution has involved the development and perfection of characters of behaviour as well as those of structure. The first step in this direction is usually the habit of protecting the eggs until the young hatch. In several species of fish, the eggs are laid in holes or in nests specially prepared by the parents, and the male remains on guard. This habit is resorted to by Proto-

pterus and Lepidosiren among the Dipnoi, by Amia, several catfish, and the stickleback, only to mention a few. In some of these cases there are interesting adaptations for ensuring a sufficient supply of oxygen to the eggs. So in Lepidosiren, the pelvic fin of the male becomes modified into a tuft-like organ well supplied with blood, from which oxygen diffuses out into the water. In some catfish, the eggs are carried about by the parent (usually the male), and so are continually exposed to fresh sea water. Ichthyophys (Gymnophiona) coils itself round its eggs in a burrow, as do some snakes such as the python. Several Anura lay their eggs in nests specially prepared ; others make living nests of themselves. In Pipa the eggs are placed on the female's back, where they sink into pits and undergo development ; the male Rhinoderma carries the eggs in large vocal sacs ; Hylambates carries the eggs in its mouth. Alytes is peculiar in that pairing takes place on land, and the eggs, which are tied together by strings of slime, are carried about by the male, wound round his legs. When the young are about to hatch, the male takes them to the water and abandons them. In some viviparous snakes such as the viper, the young remain with the parent for a time. It happens in some forms (*e.g.* viper) that the egg is hatched while still in the oviduct, without being laid. This condition is called ovo-viviparous.

The eggs of birds require a constant high temperature for their development, and this necessitates the uninterrupted attention of the parents. (In the Megapodes, the eggs are laid in heaps of decaying vegetable matter, the heat of which enables them to incubate.) Nearly all birds lay their eggs in nests, which serve to protect the eggs from enemies, cold and damp. Nests are constructions in which as a rule both sexes take part, and courtship and display play an important part in keeping together the members of a pair to perform the various duties which devolve on them. The male is usually the active partner in courtship, and often possesses brilliant secondary sexual characters used for the purpose. After the nest has been built, these duties include the collecting of food for the sitting partner, and for the young when they hatch in

a helpless condition. In some species, this food is freshly caught, in others it is regurgitated, while in the pigeon the lining of the crop comes away forming a mucous secretion known as " pigeon's milk."

In all mammals, the young are fed on milk produced by the mammary glands of the mother, and they are born alive in all except the Monotremes, in which they are hatched from eggs. The mammary glands of the Monotremes are primitive in that they do not have proper teats, but merely exude the milk which is lapped up by the young. In the Monotremes and Marsupials, the ventral surface of the belly of the female is modified to form a pouch, or marsupium. In the Monotreme, the egg is hatched in the pouch. The young Marsupial is born very early after a short period of gestation in the uterus, and in a very undeveloped condition. It becomes attached to a teat of the mammary glands which are situated in the pouch. There it completes its development. In the higher mammals, or Placentals, the allantoic placenta is well developed, and the period of gestation is long. During this time the embryo is able to develop to a high degree of perfection, such as would not be possible without a lasting physiological connexion with the mother in the form of a placenta. After birth the young is supplied with milk by the mother until it is weaned and able to feed for itself. Another feature of the mammals is that they go through a period of " childhood," during which they play, fed by the mother and protected by her and the father. Parental instincts reach their highest form in man, whose superiority in mind and body is conditioned by the relatively very great length of time spent in development, both before and after birth.

There may be one or several embryos developing in the uterus at the same time. Each embryo develops from a separate egg except in cases of true twinning ; here, as in the armadillo and possibly in man, the twins arise by a process of fission of one blastocyst which has developed from one egg.

CHAPTER XXVIII

THE HEAD AND NECK

THE structure of the head in an adult vertebrate animal is somewhat complicated, and bears little resemblance to the simpler segmented nature of the trunk-region. The segmentation is obscured, added to which there is the complication introduced by the presence of the special paired sense-organs (nose, eye, and ear) and of the gill-slits. The somites do not all form straightforward myotomes as in the trunk, but give rise to the eye-muscles; and lastly, it is difficult to recognise the segmental nerves because the dorsal and ventral nerve-roots remain separate. Nevertheless, the head is built strictly on a segmental plan, and it is easy to unravel its structure by considering early stages of development.

The embryo of the dogfish, for example, passes through a stage in which the mesoderm on each side of the body is segmented into a complete row of somites, from the front to the hind end of the body. There is no difference between the somites of the future head-region and those of the trunk, and they grade insensibly into one another. The 1st somite is, however, peculiar in that it is connected with its fellow of the opposite side by a strand of mesoderm-cells which passes in front of the tip of the notochord. Such a connexion would be impossible between somites situated farther posteriorly, because the notochord separates those of one side from those of the other. The 1st somite is called the premandibular somite, and it is innervated by a ventral nerve-root: the oculomotor. The 2nd somite is rather larger than the others, it is called the mandibular somite and is innervated by the trochlear nerve. The 3rd somite is the hyoid somite, and it is

innervated by the abducens. These first three somites will become differentiated into the extrinsic eye-muscles, and they all lie in front of the auditory vesicle, for which reason they are called the prootic somites.

The 4th somite is the 1st of the metotic somites, and it is similar to the ones following it. It and the 5th somite in the dogfish eventually disappear, being squashed underneath the large developing auditory sac, and they either do not have, or do not retain, any ventral nerve-roots. In Petromyzon, however, no somites are lost, and the 4th becomes the most
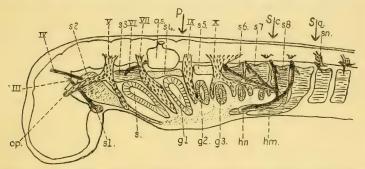
FIG. 167.—Reconstruction of the head of a dogfish embryo, showing the segmentation.

III, oculomotor; *IV*, trochlear; *V*, trigeminal; *VI*, abducens; *VII*, facial; *IX*, glossopharyngeal; *X*, vagus; nerves; *as*, auditory sac; *g1* to *g3*, first to third gill-slits; *hm*, hypoglossal muscles; *hn*, hypoglossal nerve; *op*, ophthalmicus profundus nerve; *s*, spiracle; *s1* to *s8*, first to eighth somite; *sn*, spinal nerve; the arrows show the position of the posterior limit of the neurocranium: *P*, in Petromyzon; *Sc*, in Scyllium; *Sq*, in Squalus.

anterior of the myotomes of the body. In the dogfish, it is the 6th somite which gives rise to the most anterior myotome of the body.

It is now necessary to turn to the relations which the dorsal nerve-roots bear to the somites. Above the premandibular somite, the cells of the neural crest group together to form the ganglion of the ophthalmicus profundus nerve. This nerve is lost in adult Scyllium, but it is present in Squalus, and it is the dorsal root of the 1st segment, corresponding to the oculomotor.

Above the mandibular somite is the ganglion of the trigeminal nerve which is the dorsal root of the 2nd segment, corresponding to the trochlear. The hyoid somite lies under the ganglion of the facial nerve, which is accordingly the dorsal root of the 3rd segment, corresponding to the abducens. It is possible, therefore, to recognise three prootic segments.

The glossopharyngeal nerve is the dorsal root of the 4th segment, overlying the 4th somite. The vagus represents parts of four dorsal roots joined together, and it corresponds to the 5th to 8th segments. The ventral roots of the 4th and 5th segments which disappear in the dogfish, are present in Petromyzon. The ventral roots of the 6th and following segments are present in the dogfish, innervating the anterior myotomes, and contributing to the hypoglossal nerve which accompanies the growth downwards and forwards of portions of the myotomes to form the hypoglossal muscles.

So far, then, the only difference between the head and trunk-regions is that in the former, the dorsal and ventral nerve-roots remain distinct from one another, and that in the three prootic somites the ganglia of the dorsal roots lie outside the little somites, instead of median to them as in the trunk.

It is now time to turn to the gill-slits, which arise as outgrowths from the pharynx on each side, and connect with the ectoderm. The gill-slits are formed at a level below that of the somites, in the region of the lateral plate, or unsegmented mesoderm. The connexion of the endoderm of the pharynx with the ectoderm in the formation of the gill-slits necessarily obliterates to the mesoderm in places and confines it to the bars between the gill-slits. These are the gill-bars (gill-arches, or visceral arches). The remnants of the splanchnocœlic cavity in this region are restricted to the cavities in the gill-bars (as in the primary gill-bars of Amphioxus).

Now, down each of these gill-bars or visceral arches there passes a large branch of a dorsal nerve-root. The most anterior visceral slit is the spiracle, and separating it from the mouth is the mandibular arch (or 1st visceral arch) down which the trigeminal nerve passes. Between the spiracle and the 2nd visceral slit (1st gill-slit) is the hyoid arch (or 2nd

visceral arch), and down this there passes the facial nerve.   In a similar way, the glossopharyngeal nerve passes down the 3rd visceral arch, behind the 1st gill-slit ; and a branch of the vagus runs down each of the 4th, 5th, 6th, and 7th visceral arches.

Since the dorsal nerve-roots are segmental in arrangement, the visceral arches are segmental also, for they correspond. This means that the spiracle and gill-slits are intersegmental in arrangement.   It must be remembered, however, that this segmental arrangement of the visceral arches is not the same thing as the primary and fundamental segmentation of the somites, because the visceral arches lie in the lateral-plate mesoderm (not in the segmented vertebral plate).   The cavities enclosed in the mesoderm of the visceral arches are really part of the originally continuous splanchnocœl, and not myocœlic cavities.   This is important, for it explains why the muscles to which the mesoderm of the visceral arches gives rise are innervated by dorsal and not ventral nerve-roots, although they are striped and voluntary.   Ventral nerve-roots only innervate somatic striped muscles derived from the segmented myotomes of the vertebral plate.   Muscles formed from the visceral mesoderm (inner wall of the splanchnocœlic cavity) in the region behind the gill-slits are of course the smooth muscles of the gut, innervated by the autonomic system.   That the muscles of the visceral arches should differ from these latter in being striped and voluntary is due to the fact that, unlike them, they are attached to skeletal structures.   These skeletal structures support the jaws and the branchial arches, and their movements are involved in the processes of biting and breathing, which are related to the outside world.   Smooth muscles are only related to the events which go on inside the animal.

Since the visceral arches correspond to the segmentation of the body, the structures in them correspond also.   These consist of the skeletal elements just mentioned, and of the blood-vessels which run up round the gut from the ventral to the dorsal aorta.   So Meckel's cartilage and the quadrate correspond to the trigeminal nerve and the 2nd segment, and the hyomandibula and ceratohyal correspond to the facial

nerve and the 3rd segment. The blood-vessels in these two arches disappear in the higher vertebrates, but that in the 3rd visceral arch corresponding to the glossopharyngeal nerve and the 4th segment of the body becomes the carotid. Similarly, the systemic blood-vessel corresponds to the 4th visceral arch (5th segment of the body) down which the first branch of the vagus nerve runs. The pulmonary artery corresponds to the 6th visceral arch (7th segment of the body) down which the 3rd branch of the vagus runs.

The segmentation of the head is now clear, and it may be asked how many segments of the body does the head occupy ? Before this can be answered it is necessary to be clear as to whether " the head " is to be regarded as everything in front of the hindmost part of the skull (occipital arch), or whether it extends as far back as the gill-slits. In point of fact, it is necessary to distinguish between the dorsal or " neural head," and the ventral or " visceral head," for they differ in extent. The hindmost region of the neural head is indicated by the position of the occipital arch of the skull, that of the visceral head by the position of the last visceral arch. It is interesting to find that the number of segments in either kind of " head " varies in different animals. The neural head of Petromyzon occupies 4 segments, that of Scyllium 7, that of Squalus 9, that of Amphibia 6, that of Amniotes probably 8. Similarly, the number of segments in the visceral head varies from 10 in Petromyzon to 8 in Scyllium, 9 in Hexanchus, and 10 in Heptanchus, while the number is reduced in land-vertebrates which no longer breathe by gills. In the formation of the neural head, more and more segments of the trunk are incorporated during evolution. The occipital arch is therefore not formed by the same segment in different groups of vertebrates, but this fact does not affect the homology of the occipital arches. This structure has a representative in the common ancestor of Craniates, whatever segment of the body it may be in. In the more primitive forms the neural head is short, and the occipital arch becomes displaced backwards. The primitive extent of the visceral head is probably about 10 segments, for not only is this the number in Petromyzon and

TABLE OF THE SEGMENTATION OF THE HEAD.

Segment.	Derivative of Somite.	Dorsal nerve root.	Ventral nerve root.	Visceral arch.	Branchial arch.	Skeletal elements.	Blood vessel.	Visceral slit.	Gill slit.
1 or pre-mandibular.	Rectus superior, internal, inferior. Obliquus inferior.	Ophthalmicus profundus (V 1).	Oculomotor (III).						
2 or mandibular.	Obliquus superior.	Trigeminal (V 2 & 3).	Trochlear (IV).	1st or mandibular.		Quadrate, Meckel's cartilage.	Mandibular vessel.	1st or spiracle	1st.
3 or hyoid.	Rectus external.	Facial (VII) & Auditory (VIII).	Abducens (VI).	2nd or hyoid.		Hyomandibula Ceratohyal	Hyoid vessel.	2nd.	2nd.
4.	Disappears except in Petromyzon.	Glossopharyngeal (IX).		3rd.	1st.	1st pharyngo epi, cerato, & hypo branchials.	Carotid arch.	3rd.	
5.	Disappears except in Petromyzon and Amphibia.	Vagus, 1st branch (X 1).		4th.	2nd.	2nd ditto.	Systemic arch.	4th.	
6.	1st myotome of Scyllium.	Vagus, 2nd branch (X 2).	Part of Hypoglossal (XII).	5th.	3rd.	3rd ditto.	Pulmonary arch.	5th.	3rd.
7.	2nd myotome.	Vagus 3rd branch (X 3).	Ditto.	6th.	4th.	4th ditto.		6th.	4th.
8.	3rd myotome.	Vagus 4th branch (X 4).	Ditto.	7th.	5th.	5th ditto.			5th.

in the primitive selachian Heptanchus (both of which have 8 visceral slits, although Petromyzon loses one), but Amphioxus in its development passes through a stage (the so-called " critical stage ") when it has 8 pairs of symmetrically arranged gill-slits.

The relations and destinies of the three prootic somites are constant in all vertebrates above the Cyclostomes (in which the eyes are degenerate), and they may now be considered.

In the first place, it is interesting to note that the 1st or premandibular somites correspond to the anterior head-cavities or anterior gut-diverticula of Amphioxus, and that the front ends of all chordates correspond. Just as in Amphioxus the anterior head-cavity (of the left side) opens into an ectodermal pit (the preoral pit), so in Selachians (Torpedo) the premandibular somites open into an ectodermal inpushing (the hypophysis), and this connexion between premandibular somites and hypophysis also occurs in some reptiles and birds. The hypophysis is therefore probably homologous with the preoral pit of Amphioxus. This connexion between a meso-dermal pouch and the ectoderm is similar to that which occurs in Balanoglossus and the larvæ of Echinoderms, forming the co-called " water-pores " and " proboscis-pores." (It may be mentioned that the so-called " anterior head-cavities " of some Selachians are merely parts of the premandibular somites, and have no segmental value.)

The morphological anterior end of the body in Craniates is a point near the middle of the mesodermal strand connecting the premandibular somites with one another. Just behind this point is the front end of the notochord, and the preoral gut ; just in front of it the hypophysis grows in from the superficial ectoderm, and just above it is the floor of the fore-brain near the optic chiasma and the point of closure of the neuropore. This morphologically anterior point of the animal is represented in many skulls near the dorsum sellæ, which lies immediately behind the pituitary body. That part of the head which lies in front of this is the result of secondary forward growth.

In the conversion of the prootic somites into the eye-muscles

in the dogfish, for example, the walls of the somites become thickened by the formation of muscle-fibres, and the contained cœlomic cavity is obliterated. The premandibular somite wraps round the optic nerve from behind, and becomes divided
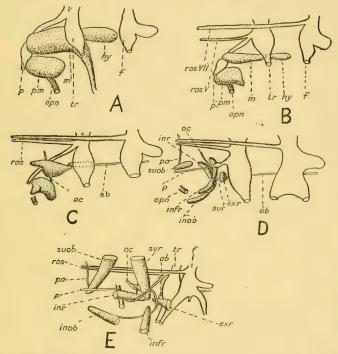
FIG. 168.—Reconstructions showing stages in the conversions of the first three somites into the extrinsic eye-muscles in a dogfish.

A to E, successive stages. *ab*, abducens ; *exr*, external rectus muscle ; *f*, facial nerve ; *hy*, hyoid or 3rd somite ; *infr*, inferior rectus muscle ; *inob*, inferior oblique muscle ; *inr*, internal rectus muscle ; *m*, mandibular or 2nd somite ; *oc*, oculomotor nerve ; *opn*, optic nerve ; *p*, profundus ophthalmicus nerve ; *pa*, trochlear nerve ; *pm*, premandibular or 1st somite ; *ros V* and *VII*, superficial ophthalmic branches of trigeminal and facial nerve ; *suob*, superior oblique muscle ; *sur*, superior rectus muscle ; *tr*, trigeminal nerve.

into four pieces. The two dorsal portions are the internal and superior recti muscles, the two ventral portions are the inferior oblique and the inferior rectus muscles. The mandibular somite grows forwards above the premandibular and gives

rise to the superior oblique; and the hyoid somite, also growing forwards, becomes attached to the posterior part of the eyeball, forming the external rectus muscle.

In higher vertebrates, the prootic somites are not always separately recognisable as such, and in these cases the eye-muscles appear to arise from masses of mesenchymatous mesoderm-cells. In others, the manner of development is the same as that described for the dogfish.

In the lower vertebrates, the head has no greater mobility than any other part of the body ; indeed, in several bony fish it has none, for the back of the skull is connected with the pectoral girdle by a chain of bones. The neck has not yet evolved in these animals. The neck is a region of flexibility which enables the head to be moved without moving the body. This is made possible by the specialisation of the most anterior vertebræ. In reptiles, the differentiation of the first two vertebræ into the atlas and axis appears, and the head is then able to hinge on the transverse axis (as in signing "yes"), and on the longitudinal axis (as in signing " no "). Movement of the head to the side is effected by the flexibility of the next posterior vertebræ, the ribs of which do not get attached to the sternum. In this way, the cervical vertebræ differ from the thoracic. When the neck is very long and capable of extensive twisting, it is common to find vertebrarterial canals, formed between the centra and the ribs fused on to them. These canals protect the artery from being kinked when the neck is twisted. In mammals, the neck contains seven vertebræ, except in three species only.

LITERATURE

GOODRICH, E. S. " Proboscis Pores " in Craniate Vertebrates. Quarterly Journal of Microscopical Science, vol. 62, 1917.

—— On the development of the Segments of the Head in Scyllium. Quarterly Journal of Microscopical Science, vol. 63, 1918.

VAN WIJHE, J. W. Ueber die Mesodermsegmente und die Entwicklung der Nerven des Selachierkopfes. de Waal, Groningen, 1915.

CHAPTER XXIX

It is usual to describe and to refer to a nerve with regard to the segment of the body in which it finds itself. So one may speak of the facial (7th) nerve, or of the 2nd spinal nerve, and designate by these terms well-marked structures, visible by dissection. Nerves are composed of fibres formed of long filaments (or axons) which are produced by cells (neurons), the " bodies " and nuclei of which are situated in the brain and spinal cord, or in the swellings on certain nerves, called ganglia. But all the fibres of any given segmental nerve do not serve the same function. The function of a nerve is to conduct impulses. If the conduction is towards the brain and spinal cord (which together are called the central nervous system) from sense-organs, the fibres are called afferent or sensory. If the conduction is from the central nervous system outwards towards muscles or glands, the fibres are called efferent or motor. Sense-organs may be of many different kinds and appreciate various sorts of stimuli, such as light, sound, pressure, vibration, pain, etc., but from the fact that they do receive these stimuli they are called receptors. On the other hand, muscles and glands are structures which " do something," and are consequently called effectors.

A large part of the life of an animal is taken up with adjusting itself to different conditions, and these conditions may be of two kinds. There is the outside world with which the animal keeps in touch by means of its receptors at or near the skin : eyes, ears, lateral-line organs, and the skin itself. These are the exteroceptors. The movements which the animal makes in response to the outside world are largely locomotory, and brought about by the muscles of the body-wall and limbs.

These muscles are striated and voluntary. In order that such movements may be properly coordinated, the animal must have some information (unconscious, of course) of the existing state of its muscles, tendons, and joints. This is supplied by sense-organs which are situated in these structures, and are called proprioceptors.

At the same time, there is a " world " within the animal, and sensations arise from stimuli which start from organs
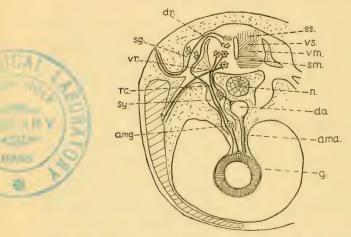
Fig. 169.—Diagrammatic transverse section through the trunk of a verte-brate showing the relations of the nerve-roots, sympathetic ganglia, and the functional components.

ama, anterior mesenteric artery ; *amg*, anterior mesenteric ganglion ; *da*, dorsal aorta ; *dr*, dorsal nerve-root ; *g*, gut ; *n*, notochord ; *rc*, ramus communicans ; *sg*, spinal ganglion ; *sm*, somatic motor region of grey matter ; *ss*, somatic sensory region ; *sy*, sympathetic ganglion ; *vm*, visceral motor region ; *vr*, ventral nerve-root ; *vs*, visceral sensory region.

such as the stomach, intestine, or bladder, and the functions connected with them. The sense-organs of taste are largely of use in connexion with what is about to enter the alimentary canal, and they also belong here. Such sense organs are called interoceptors. The reactions to these stimuli take the form of secretions on the part of glands, and contractions of the muscles of the alimentary canal, bladder, arteries, or oviduct. Such muscles are always smooth and involuntary.

It is possible, therefore, to make out four main divisions of the nerves according to their function :

those which convey sensory impulses from the outside world, somatic sensory, or afferent ;

those which convey sensory impulses from the inner world, visceral sensory, or afferent ;

those which convey motor impulses to the smooth muscles of the viscera, visceral motor, or efferent ;

those which convey motor impulses to the striped muscles of the body-wall and limbs, somatic motor, or efferent.

Each of these functional systems are called components, and as the same components can be found in several different nerves, it is interesting to study the nerves according to the components which they contain. In this way a classification of nerves is obtained which, as it were, runs at right angles to the classification according to the segment of the body in which they lie. Further, the different components occupy special parts of the central nervous system, and the evolution of the latter, and especially of the brain, has been largely controlled by the positions and relations of these " centres."

In an ordinary spinal nerve of any vertebrate above the Cyclostomes, there are two roots : one dorsal and one ventral, and they join to form a mixed nerve. The mixed nerve also sends a branch (ramus communicans) to a sympathetic ganglion. Now, the dorsal root is made of fibres of afferent (sensory) neurons, and the ventral root is composed of efferent (motor) ones. Accompanying the anatomical division into dorsal and ventral roots, there is therefore an important physiological distinction.

The cell-bodies of the afferent neurons are situated in the ganglion which is always present on the dorsal root in all chordates above Amphioxus. This means that the receptor cell itself does not convey the impulse to the central nervous system, this function being served by the afferent neuron of the ganglion of the dorsal root. (In Amphioxus, and in the nose of all vertebrates, on the other hand, the primitive condition characteristic of many invertebrates persists : that is, the receptor sensory cell itself produces an axon which runs

into the central nervous system and conveys the impulse thither. There is, therefore, no ganglion on the dorsal root of the nerves of Amphioxus, nor on the olfactory nerve in any vertebrate.)

After running into the central nervous system through the dorsal root, the afferent fibres terminate and make synaptic connexions with other neurons. Now the neurons in the spinal cord have their cell-bodies in the grey matter which is central, while the surrounding white matter is made up of the axons (fibres) which pass up and down the cord to higher or lower levels. The grey matter of the cord can be separated into four longitudinal regions on each side. The most dorsal strip is where the fibres of somatic afferent neurons terminate. Beneath this is the place where the visceral afferent neurons end. Under this again is the region which contains the cell-bodies of the efferent visceral neurons ; and lastly the most ventral part of the grey matter contains the cell-bodies of the efferent somatic neurons. Thus the dorsal half of the spinal cord is related to afferent and the ventral half to efferent fibres. As will be seen later, this arrangement is also the fundamental plan on which the brain is built.

The axons of the efferent neurons run out of the spinal cord through the ventral root. The somatic efferent neurons go straight to the striped voluntary muscles of the body-wall, and to the muscles of the limbs (or fins) and end in them. All muscles which are innervated direct in this way by ventral roots are somatic, striped, voluntary muscles derived from the segmented myotomes. On the other hand, the visceral efferent fibres leave the mixed nerve by the ramus communicans, and end in the sympathetic ganglia. There they make synaptic connexions with other neurons which run to the smooth muscles of the viscera and form the sympathetic (autonomic) nervous system. The sympathetic system will be dealt with in greater detail below, but it may be noticed now that the visceral efferent fibres belonging to this system never run all the way to the smooth muscle or gland. There is always another neuron intercalated in the circuit, and carrying the impulses on from the sympathetic ganglion. The

muscles so innervated are never striped, voluntary nor derived from the segmented myotomes.

The ramus communicans serves not only for the passage of the visceral efferent fibres, but also for the visceral afferent fibres, which then continue to the spinal cord through the dorsal root.

In the region of the head, a slight complication is introduced owing to the development of special sense-organs, and to the fact that the anterior region of the alimentary canal is modified in connexion with the jaws and gill-arches. There is further the fact that the dorsal and ventral nerve-roots of the cranial segments remain separated and do not join to form a mixed nerve.

The various nerve-components in the head can conveniently be studied in the dogfish. Leaving aside for the moment the very specialised visual and olfactory organs, the somatic afferent system is divided into two owing to the development of the lateral-line system.

There is, therefore, a general somatic afferent system which receives impulses from simple sense-organs in the skin corresponding to those in the region of the trunk and spinal nerves. This component is present in the trigeminal, glossopharyngeal, and vagus, and their fibres end in the dorsal portion of the medulla oblongata in a region which may be called the " skin-brain."

The special somatic afferent system is concerned with the lateral-line organs and the special member of these which is the ear. This component is present in the facial (superficial ophthalmic, buccal and hyomandibular branches), auditory, glossopharyngeal and vagus, and its centre is also in the dorsal part of the medulla oblongata. So great is the number of fibres which end in this way, that the neurons in the medulla with which the afferent fibres make connexion are also multiplied. The result is that this region, which may be called the " ear-brain," bulges out, forming the tuberculum acusticum. The special somatic afferent system is also called the lateralis system, and arises in relation to the dorso-lateral placodes of the 7th, 9th, and 10th cranial nerves (see p. 194).

The proprioceptive organs are innervated by nerves which (in the head) run in to the brain through most of the cranial nerves, including the oculomotor, trochlear, and abducens. The ear, as an organ of balance, can also be considered as belonging to the proprioceptive organs.

The visceral afferent fibres collect impulses from the mucous surface of the pharynx, mouth, and other viscera, and from the taste sense-organs. In fish, the taste sense-organs are not confined to the mouth, but may be found all over the surface of the body. The afferent visceral fibres run in the branches of the facial, glossopharyngeal, and vagus from the pharynx and from the anterior and posterior faces of the gill-slits. In the brain they converge in the medulla oblongata in the visceral lobe or " taste-brain," beneath the centres for the somatic afferent system. The visceral afferent system is also called the communis system. The fibres innervating the sense-organs of taste are sometimes regarded as forming the special visceral afferent system, and they arise in relation to the epibranchial placodes (see p. 194).

The visceral efferent system is complicated by the fact that the anterior end of the alimentary canal enters into relations with the outside world. Its opening, the mouth, is bounded by the jaws which are under voluntary control, and so enable the animal to aim at its prey and bite it. In connexion with this, it is found that the muscles which actuate the jaws are striated and voluntary, although they are visceral in origin. The muscles attached to the gill-arches and which perform respiratory movements are likewise striated. But although voluntary and striated, these jaw and gill-arch muscles are not innervated by ventral roots, for they are not derived from segmented myotomes. Instead, they are innervated direct by fibres of the special efferent visceral system which run in the branches of the trigeminal, facial, glossopharyngeal, and vagus, that pass down behind the mouth, spiracle, and the several gill-slits respectively. In higher vertebrates, a portion of the fibres of the vagus become grouped together more posteriorly, and form the spinal accessory or 11th nerve.

The general efferent visceral system innervates smooth
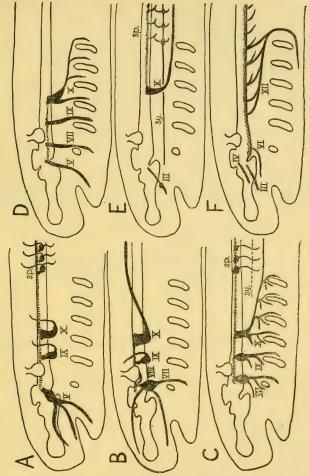
FIG. 170.—Diagrammatic representation of the component systems of the nerves of a dogfish (based on Herrick and Johnston).

A, general somatic sensory (exteroceptive); B, special somatic sensory (from lateral-line organs and ear); C, visceral sensory (in the trunk-region the nerves pass through the sympathetic chain); D, special visceral motor (to the striated visceral muscles of the visceral arches); E, visceral motor (autonomic); F, somatic motor; G, see p. 370. The cranial nerves are indicated by Roman figures: *sp*, spinal nerves; *sy*, sympathetic chain. The regions of the brain and spinal cord which are related to the various component systems are shaded.

2 B

muscles and glands, and forms part of the autonomic (parasympathetic) system. The fibres run through the oculomotor, facial, glossopharyngeal, and vagus nerves. The centre of origin of the visceral efferent neurons is for the most part in the medulla oblongata, beneath the visceral lobe.

The somatic efferent system is concerned with the innervation of striated voluntary muscles derived from the segmented myotomes. In the head these are represented by the muscles which move the eyeballs, and the hypoglossal muscles. This component is, therefore, to be found in the oculomotor, trochlear, abducens, and hypoglossal nerves. The centres of the oculomotor and trochlear are in the mid-brain, those of the abducens and hypoglossal are in the medulla oblongata.
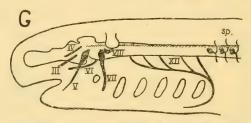
Fig. 170, G.—The proprioceptive fibres of the general somatic sensory component.

It may be noticed that the arrangement in the medulla oblongata of the centres concerned with the various components, is similar in a general way to that which holds in the spinal cord. The medulla is the least specialised portion of the brain.

The eyes themselves are part of the brain, and therefore the optic nerve is not an ordinary nerve. Its fibres are strictly intra-cerebral throughout their course. They run through the optic chiasma and end in the roof of the midbrain, which is enlarged to form the optic lobes, or " eye-brain."

The nasal sacs are lined by sensory epithelium, the cells of which produce axons growing back into the end-brain. The latter becomes enlarged to form the olfactory lobes or " nose-brain."

Expressed in tabular form, the component nerve-systems are as follows :—

Somatic.	Afferent.	General.	Exteroceptors
			Proprioceptors ⎫ ear.
		Special.	Lateral-line organs ⎰
	Efferent.		To myotomic striped muscles.
Visceral.	Afferent.	Interoceptors.	Taste organs and mucous surfaces.
	Efferent.	General.	Autonomic (sympathetic and para-sympathetic) to smooth muscles and glands.
		Special.	To striped visceral muscles of jaw and gill-arches.

Eye.
Nose.

LITERATURE

HERRICK, C. JUDSON. An Introduction to Neurology. Saunders Co., Philadelphia and London, 1922.

JOHNSTON, J. B. The Nervous System of Vertebrates. John Murray, London, 1907.

CHAPTER XXX

THE brain is the anterior region of the spinal cord, modified, specialised, and enlarged in connexion with the development of special sense-organs in the anterior region of the body. That these sense-organs should be accumulated here rather than elsewhere is due to the fact that chordate animals are bilaterally symmetrical and move along a definite axis with one end constantly leading. This end is the first to come into contact with new surroundings, information concerning which is of the highest value to the animal.

In order to understand the evolution of the spinal cord and brain, it is necessary to consider what is known as a reflex arc. An afferent fibre brings an impulse from a receptor, and if this afferent fibre were to connect with only one efferent fibre going to a particular muscle, whenever the receptor was stimulated the response would be the contraction of this muscle. Nothing else in the way of response would be possible. But actually the afferent fibre when it has run into the brain or spinal cord makes a large number of connexions with other neurons. Some of these may be efferent neurons and connected with various effectors ; others may be neurons which carry the impulse to other parts of the spinal cord or brain : the so-called association-neurons. By this means a receptor can be connected up with several effectors, or one effector may be stimulated by impulses coming from several different receptors. This possibility of one efferent neuron being used by impulses coming from several afferent neurons, as a " final common path " for their reflex circuits, is of the greatest importance. The efficiency and economy of using what may be called

interchangeable standard units (the neurons), capable of an infinite variety of combinations is one of the main factors of the success of the higher vertebrates. An animal possessing this type of nervous system can make many kinds of response, and indeed by suitable connexions and adjustments there is no limit to the number of combinations which may be formed between receptors and effectors. These adjustments are made in the central nervous system, and they are its function, just as that of a telephone exchange is to make adjustments between calling and answering subscribers. The key to the whole system is the neuron, which is not rigidly fused on to any other cell, but which can make synaptic connexions with a great number of other cells and pass impulses on to them. New connexions can be made, and new kinds of response can be evolved, which become " conditioned " reflexes, or habits.

The places in the central nervous system where these adjustments are made are called centres, and they lie in the grey matter. When the skin of a dog is stimulated by a small irritation, the receptor in the skin sends an impulse through an afferent neuron which runs into the spinal cord by the dorsal root. This neuron makes a synaptic connexion with an association-neuron in the grey matter of the spinal cord. The fibre of this association-neuron runs down the spinal cord in the white matter to the segment of the body where the hind leg is situated. There it makes a synaptic connexion with an efferent neuron (in the grey matter) which passes out through the ventral root to the muscle of the leg. The result of the stimulus is a jerk or " scratch " on the part of the leg. This reflex arc illustrates the fact that the function of the spinal cord is twofold. It contains a number of reflex adjustment-centres (in the grey matter), and it conducts impulses up or down the cord to different levels (in the white matter).

In the brain there are the primary centres, connected with the different functional systems of components. These are the " skin brain," " ear-brain," " taste-brain " (in the medulla oblongata), the " eye-brain " (in the midbrain) and the " nose-brain " (in the forebrain). Each of these is a centre where impulses are received of a particular type (from a particular

component-system), and where adjustments are made with association and efferent neurons so as to complete the reflex circuit.

Now if these primary centres are marked off in the brain of a dogfish, it is found that except for the cerebellum, they occupy nearly the whole of the brain. Those regions of the brain which conform to the organisation of the spinal cord are called the " segmental apparatus " or " brain-stem," and are
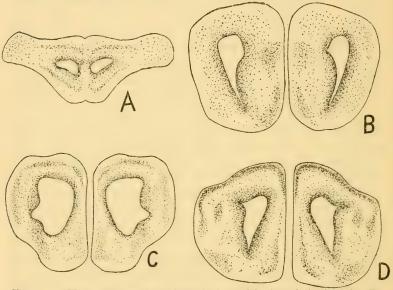
FIG. 171.—Transverse sections through the end-brains of, A, dogfish ; B, frog ; C, Chelonian (reptile) ; and D, shrew (mammal).

Showing the development of the cerebral hemispheres and lateral ventricles, and the migration of nerve-cells to the surface forming a cortex.

to be distinguished from the additions in the shape of the cerebellum, and in higher forms the cerebral cortex, which are " suprasegmental " structures.

The various centres of the brain of the fish are mainly concerned with their own functional component-system ; there is not much " team work " between the different centres. The result is that the behaviour of fish largely takes the form of reflex responses to stimuli of certain kinds without much

ability for variation or modification by experience. When any particular sensory system is very highly developed, the corresponding centre in the brain is enlarged. So in the carps, which are well supplied with taste-organs, the medulla oblongata is enlarged owing to the expansion of the visceral lobe. This expansion is due to the increase in number of neurons in the centre, parallel with the increased number of afferent fibres coming from the numerous receptors. In the catfish, the lateral-line system and the " ear-brain " are well developed.

A certain amount of correlation exists between the primary centres. For example, in the catfish, the " skin-brain " is connected with the " taste-brain," so that food may be recognised by touch and by taste, and these two types of sensation co-operate in producing those movements which lead to feeding. In other words, the reflex arc can pass from one functional component system to the other.

But this interrelation and team work between primary centres is best brought about by special correlation-centres, which are not related to any single primary centre but to several. The history of the development and evolution of these correlation-centres really makes up the evolution of the brain in vertebrates.

In the fish, the correlation-centres are not well developed, with the exception of the cerebellum. The cerebellum lies on the dorsal side of the medulla, and from its position its connexions are mostly with the neighbouring centres : " ear-brain " and " eye-brain." The ear-brain is concerned with the balance of the animal as reported from the semicircular canals, and the eyes report its position relatively to external objects. At the same time, fibres of the general somatic system run to the cerebellum and convey impulses of tactile sensations, and of the state of the muscles and joints of the body (proprioceptive). As a result of the commingling of these impulses, the cerebellum comes to be an organ for the regulation of the posture of the body and of bodily movements. It keeps the muscles in " tone," and as a whole regulates the execution of reflexes. It may, in a sense, be compared with the steam steering gear of a ship, which smoothly carries out

the directions of the man at the wheel ; and it has been called the head of the proprioceptive system.

In bony fish, the cerebellum is enlarged to form the so-called valvula which projects forwards beneath the roof of the midbrain. In most amphibia and all higher vertebrates the lateral-line system is lost except for the ear, and the cochlea or organ of hearing is better developed. This affects the cerebellum to some extent. In mammals two new features arise, the superficial cerebellar cortex and the pons Varolii. These develop in connexion with the cerebral cortex.

Apart from the cerebellum, the correlation-centres are mostly concerned with responses to the outside world. In the fish there are correlation-centres of this kind in the forebrain and the midbrain, but the most important are those which become evolved above the evolutionary stage of the fish, and which are situated in the sides of the between-brain (thalamus), the floor of the end-brain (corpus striatum), and the roof of the end-brain (cerebral cortex).

It is characteristic of these higher centres of correlation that they are more or less isolated from the primary sensory centres ; in other words, the correlation-centres are not mono-polised by any single sensory system. In much the same way, if the government of a nation sat in the ordinary town-hall of one of its cities, much of its business would be taken up or influenced by local municipal matters, and it would be less able to deal with business affecting not the city but the nation as a whole.

The thalamus is related by fibres to most of the sensory centres, and it is among other things the centre where impulses are analysed into pleasurable and painful. As such, it is of great importance, for a negative reaction to danger and a positive reaction to food and to a mate go far to ensure the perpetuation of the species. Consequently the thalamus has great survival value in evolution.

The corpus striatum reaches a great development in birds, in which it is responsible for the correlation of the many and varied reactions and movements which form part of the instinctive behaviour. Instinct in birds is highly developed,

and its hereditary nature is due to the fact that the reflex arcs and association-neurons in the thalamus and corpus striatum
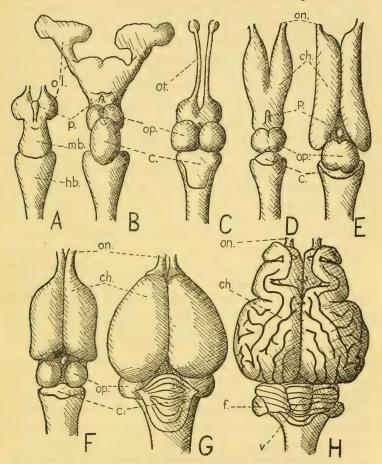
FIG. 172.—Dorsal views of the brains of A, Petromyzon ; B, Scyllium ; C, Gadus ; D, Ceratodus ; E, Triton ; F, Lacerta ; G, Columba ; and H, sheep. (Not all drawn to the same scale.)

c, cerebellum ; *ch*, cerebral hemisphere ; *f*, flocculus ; *hb*, hindbrain ; *mb*, midbrain ; *ol*, olfactory lobe ; *on*, olfactory nerve ; *op*, optic lobe ; *ot*, olfactory tract ; *p*, pineal ; *v*, vermis.

conform to a certain pattern which is the result of development. This also accounts for the fact that instincts are specific, that

is, they occur in all members of a species, just as they all have kidneys or livers. But because instinct is determined by the hereditary pattern of the neurons, such behaviour is not easily modified to meet unusual circumstances. A good example of such shortcomings is to be found in the meadow pipit, a bird which is parasitised by the cuckoo. In the pipit's nest the cuckoo lays an egg, which hatches into a young cuckoo. This young parasite proceeds to eject the young pipits from the nest. It was observed on one occasion that the young pipit so ejected remained just outside the nest, under the mother-bird's nose, where it lay helpless and squeaking. It never occurred to the mother-bird to put it back in the nest under her, and so the young one died. The situation was novel and had not presented itself to the bird before, and it could not rise to the occasion. The necessary correlation of neurons could not be made ; and if it could, the bird would probably not have been able to act on the experience of a similar previous occasion. The corpus striatum is not well adapted for such powers of individual adaptability, though it is very suitable for ready-made correlations which make the species as a whole well adapted to a particular routine of life. It is interesting to note that the behaviour of birds resembles that of insects in this respect, and that both the brain of the insect and the corpus striatum of birds are solid compact masses of neurons. For really effective and unusual correlations such an arrangement appears to be ill suited. The cerebral cortex which fulfils this very function is shaped not as a solid mass, but as a layer of neurons, the number of which is augmented by increasing the area of the layer. The hollow tubular nerve-cord of vertebrates is very suitable for such an arrangement, and it is probable that its possession enabled vertebrates to evolve as they have done, while its absence from insects prevented them from progressing any further.

The cerebral cortex is a layer of grey matter near the surface of the end-brain. It is scarcely represented in the fish, and in the amphibia most of the neurons remain in the primitive position for grey matter ; that is, near the central cavity. Some neurons, however, migrate towards the surface. At

the same time, the end-brain has been evolving in another direction, in that the cerebral hemispheres are formed as outgrowths containing each a cavity (the lateral ventricles) communicating with that of the between-brain through the foramina of Monro.   Cerebral hemispheres first appear in the Dipnoi, and it is possible that they are an adaptation to deficient oxygen-supply : a matter of great importance, for the brain requires the purest arterial blood in the body.   The formation of cerebral hemispheres increases the surface of the brain-tissue relatively to its volume, not only on the outside in contact with the vascular pia mater, but also on the inside which is bathed by the cerebro-spinal fluid, itself oxygenated by the choroid plexus.   The migration of the neurons to the surface to form a cortex may also be an adaptation to oxygen require-ments, for solid masses of neurons would require large arteries to enter the brain, and there are indications that the pulse of large arteries is injurious to the delicate workings of the neurons.

Another advantage of the cortex type of structure is that it allows of the arrangement of centres on its surface after the fashion of a chequer board.   The cortex deals with impulses from the outside world, in animals with sense-organs sufficiently well developed to give them good representations of the relations of different objects and events in space.   It is apparently necessary that these representations of objects in space should remain separate in the brain until finally co-ordinated.   In the same way it would be impossible to judge which of a number of threads was which, if they were all tangled up together in a ball.   This analogy also introduces the fact that the function of the cerebral cortex is to receive the impulses which have already been sorted out in the correlation-centres, and to judge which of many possible is the best response to make.   The cortex introduces hesitancy and arbitration into behaviour, which, on the level of the reflex arc, is immediate and determined.

Another factor to be borne in mind is that the cerebral cortex is principally concerned with impulses coming from the exteroceptors, and especially those which, like the eye,

ear, and nose, can perceive objects at a distance : the distance-receptors. Responses to stimuli which touch the animal usually (when successful) abolish the stimulus which evoked them. So the flea tickling the dog on its skin evokes the scratch which incapacitates the flea from tickling any more. Such a response is consummatory. If, however, an animal sees some of its food at a distance, the response which it makes to start with does not abolish the stimulus. It sets its limbs in motion towards the food ; this is an anticipatory response, and the consummation is not complete until the food has been reached and eaten. Until this time, the food occupies the attention of the animal.

In the reptiles, there are three sheets of superficial grey matter in each cerebral hemisphere. The median sheet is the hippocampal and the lateral sheet the pyriform cortex. Both these regions are predominantly concerned with impulses coming from the nose ; they are not really " impartial " arbitrators of behaviour. That the cerebral hemispheres should in early stages of evolution be largely under the influence of olfactory sensations follows from the proximity of the olfactory lobes, and from the fact that at these stages the vertebrates had recently emerged from life in water to dry land, for the nose is a more highly developed and efficient organ in air than in water. Being at the most anterior end of the brain, it naturally took time in evolution before fibres from all the correlation-centres farther back in the central nervous system reached them. Part of the middle sheet in the cerebral hemispheres of the reptile appears to be the forerunner of the true cerebral cortex, which reaches such a high development in the mammals. The hippocampal and pyriform cortex are called archipallium, to distinguish them from this neopallium in which olfactory impulses do not predominate.

In the birds the cerebral cortex is less well developed than in the reptiles, and the corpus striatum with the attendant highly instinctive type of behaviour is specialised instead.

In the mammals, the cerebral cortex is developed out of proportion to the rest of the brain. In the higher mammals (but not in Monotremes or Marsupials) a special commissure

is developed to link together the neopallium of the two hemi-
spheres ; this is the corpus callosum.   The dorsal commissure
of the reptiles, which links together the hippocampal archi-
pallia, persists in the mammals as the hippocampal commissure.

The volume of the neopallium is increased in higher
mammals without much increasing its thickness by throwing
it into folds.

The various regions of the neopallium are connected with
the other centres by projection-fibres, and in addition, these
regions are interconnected by association-fibres.   The number
of possible combinations between the neurons is so large that
it baffles the power of the mind to grasp it.   As an example,
one million neurons connected together in all possible ways
in groups of two neurons each, gives a number of combinations
with nearly three million figures in it.   There are not far off
ten million neurons in the human cerebral cortex.

The neopallium is therefore well fitted to correlate all the
stimuli which the animal receives and to make delicately
adjusted responses to them.   It also serves as a storehouse
for impressions which are collected during experience, and an
animal which, in determining the response to be made to a
set of stimuli, considers the results of experience, is said to
show intelligent behaviour.   Such an animal has the power of
learning, which is not the same thing as the establishment of
a habit.   Habits can be formed in the lower simple correlation-
centres, by means of neurons between certain afferent and
certain efferent neurons.   The oftener an impulse passes
along a reflex arc the easier does its passage become, with the
result that the " habitual " response is given to a stimulus.
Some habits so formed may be quite complicated, as when
a piece of music is " learned by heart."   This learning is,
however, not necessarily intelligent, because it often happens
that when the musician breaks down he is unable to adapt
himself to the immediate circumstances and continue, but
has to start again at the beginning.

In a similar way animals can be trained to do tricks, or to
thread the " Hampton Court " maze without going down any
of the blind alleys.   If a rat be so trained as to " know " a

maze perfectly, and then be placed in a similar maze but with different lengths of alleys and distances between the turnings, it will try to run the distances which it ran in the original maze, and turn where the turnings were in it, and in so doing it bumps into the walls of the new maze. Its learning was therefore not intelligent.

It is interesting to compare this case with that of a chimpanzee confronted with a novel situation. In order to reach food which was placed out of its reach, it hit suddenly on the idea of piling packing-cases on one another and climbing up on them. There is a good deal of evidence to show that in order to " see " what to do in a set of circumstances, the ape must really see the goal and the object which it may use as an instrument, in the same field of view at the same time. There is little doubt that the eyes have played an important part in the evolution of the brain : in man the number of afferent fibres running in from the retina is greater than that running in from all the spinal nerves of one side put together.

The possession of a cerebral cortex and neopallium does not adapt the species to any particular set of environmental circumstances, but instead, it makes all the members of the species individually adaptable to a large variety of circumstances. This is one of the chief differences between the higher and lower vertebrates. All are well supplied with sense-organs, but the lower vertebrates can only make a small number of kinds of responses to the stimuli which they receive. The higher vertebrates have much the same amount of information given them by their sense-organs, but they use it to much better advantage owing to the integrative and retentive properties of the neopallium. The intelligent being does not waste time on trial and error like Paramecium ; the probable results of possible actions are weighed up in what must be called the mind, with the help of experience stored up as memory, and by means of thought, and the action when taken is intentional. Lastly, it must be noticed that the possession of such a mind and its physical basis the neopallium, confers an enormous advantage on its possessor, and has survival value in evolution.

LITERATURE

ELLIOT SMITH, G.   Some Problems Relating to the Evolution of the Brain. The Lancet, 1910 (1), pp. 1, 147, and 221.

HERRICK, C. JUDSON.   Brains of Rats and Men.   University of Chicago Press, 1926.

——.   Neurological Foundations of Animal Behaviour.   Henry Holt & Co., New York, 1924.

KÖHLER, W.   The Mentality of Apes.   Kegan Paul, London, 1925.

KUHLENBECK, H.   Vorlesungen über das Zentralnervensystem der Wirbeltiere.   Fischer, Jena.   1927.

SHERRINGTON, C. S.   The Integrative Action of the Nervous System.   Yale University Press, 1920.

SMITH, E. M.   The Investigation of Mind in Animals.   Cambridge University Press, 1923.

CHAPTER XXXI

THE AUTONOMIC NERVOUS SYSTEM

It has been mentioned that the smooth muscles and glands of the body are innervated by fibres of the general visceral efferent component system. It is characteristic of such fibres that they do not reach all the way from the central nervous system to the effector in question, but they make synaptic connexions with other neurons which carry the impulses on to the muscle or gland as the case may be. There are, therefore, two members in each efferent circuit of this kind : a connector neuron and an exciter neuron. The cell-body of the exciter neuron may be in a sympathetic ganglion, or it may be by itself near the muscle which it innervates. In the former case, the connector neuron is often called the preganglionic fibre, and the exciter the postganglionic fibre. Impulses conveyed in this way through the visceral efferent system to smooth muscles and glands are involuntary, and the neurons and ganglia concerned in the conduction of these impulses form the autonomic or involuntary nervous system. It may be noticed that the autonomic system is essentially efferent. Although the afferent visceral neurons run up from the viscera through the ramus communicans, and accompany the efferent neurons, they conform to the type of the somatic afferent fibres in that their cell-bodies are in the ganglia on the dorsal roots, and that they stretch all the way from the sense-organ to the central nervous system. After separating off the autonomic nervous system, what is left is called the cerebro-spinal nervous system, including the brain, spinal cord, and the somatic fibre-systems.

The autonomic nervous system can be separated into two divisions, each of which works against the other. The visceral

efferent fibres which come out from the spinal cord in the neck, thorax, and lumbar regions together constitute the sympathetic system ; those which leave the central nervous system in the head from the brain, and from the spinal cord in the sacral region, constitute the parasympathetic system. The word " sympathetic " is sometimes loosely used as synonymous with " autonomic," which introduces confusion. The sympathetic system may be called the " thoracico-lumbar " outflow, and the parasympathetic system the " cranio-sacral outflow."

The autonomic system may now be described in greater detail, in a typical mammal, and commencing with its sympathetic constituent.

The visceral efferent fibres in the cervical, thoracic and lumbar regions of the spinal cord run out through the ventral roots and down the rami communicantes to the sympathetic ganglia situated on each side of the aorta. These fibres are preganglionic or connectors, and their cell-bodies are in the grey matter of the spinal cord ; they are surrounded by medullary sheaths and these rami communicantes are consequently white.

Some of the preganglionic fibres stop in the sympathetic ganglion corresponding to the segment in which they emerge from the spinal cord, others continue to the next sympathetic ganglia in front or behind and end there. In this way, the sympathetic ganglia of each side become connected together forming the lateral sympathetic chains, and the ganglia on them are called the lateral ganglia. In the region of the neck, several of these lateral ganglia join up close together, forming the large anterior and posterior cervical ganglia and the stellate ganglion.

Yet other preganglionic fibres run out through the lateral ganglia, but do not stop there. Instead, they run on and end in groups of ganglia situated near the base of the cœliac, anterior and posterior mesenteric arteries. The most important of these ganglia, which are called collateral, are the anterior mesenteric and the posterior mesenteric ganglia. The long rami communicantes which connect these ganglia with the spinal nerves are the splanchnic nerves.

In the lateral and collateral sympathetic ganglia are the cell-bodies of the postganglionic or exciter neurons. These run out of the ganglia as non-medullated and therefore grey fibres, to the muscles of the blood-vessels, heart, stomach, intestine, oviduct, bladder, and skin ; and some of them run to the ciliary and iris muscles inside the eye.

The effect of stimulation through the sympathetic system is to slacken the ordinary muscles surrounding the gut, but to tighten the sphincters, to tighten the heart and artery muscles, to tighten the muscles under the skin (which make hair stand " on end "), to tighten and slacken the muscles of the oviduct, to slacken the sphincter and tighten the radial muscles of the iris so that the pupil enlarges.

The structures enumerated above are also innervated by the parasympathetic system (except the muscles of the oviduct). The visceral branch of the vagus contains connector fibres which run to exciter neurons situated on the lungs, heart, and the muscles of the gut as far as the end of the small intestine. In the region of the intestine, the exciter neurons lie between the muscle coats of the gut, forming the plexus of Auerbach. The remainder of the gut is innervated by connector fibres which leave the spinal cord in the sacral region through the ventral nerve-roots, and form the pelvic nerve. These connector fibres run to exciter neurons on the muscles of the large intestine, on the bladder, on the skin round the anus, and on the blood-vessels near the urethra.

The ciliary and iris eye-muscles receive innervation by means of connector fibres which run in the oculomotor nerve to the ciliary ganglion. This ganglion contains the cell-bodies of the exciter neurons which run to the muscles in question in the eye. Two sets of autonomic connector fibres run through the facial nerve. One goes down the palatine branch (" greater superficial petrosal ") to the spheno-palatine ganglion from which exciter neurons run to the lachrymal glands and the glands of the nose. The other set runs in the chorda tympani (ramus mandibularis internus facialis of the dogfish) to the submaxillary ganglion, whence exciter neurons run to the submaxillary salivary glands. Another set

of connector fibres runs out in the glossopharyngeal nerve through the lesser superficial petrosal nerve to the otic ganglion, from which exciter neurons innervate the parotid salivary glands.

A very interesting feature of the connector fibres of the parasympathetic autonomic nervous system is, that while those of the oculomotor (midbrain outflow) and of the sacral outflow connect with the central nervous system through ventral nerve-roots, those of the facial, glossopharyngeal, and vagus (hindbrain outflow) run in dorsal nerve-roots.

The anatomy of the autonomic system in the head is slightly complicated. The anterior prolongation of the lateral sympathetic chain of the trunk continues forwards, accompanying the internal carotid artery as the internal carotid nerve. A branch of it (the deep petrosal) joins the palatine nerve (forming the Vidian nerve) and runs to the spheno-palatine ganglion. This ganglion is also connected to the maxillary branch of the trigeminal. Another sympathetic branch runs to the ciliary ganglion, which is also connected to the ophthalmic branch of the trigeminal. The sympathetic exciter neurons from the anterior cervical ganglion are thus able to make their way into the eye to the iris-muscles. The mandibular branch of the trigeminal connects with the chorda tympani and the sub-maxillary ganglion.

Further mention must be made of Auerbach's plexus, which lies between the circular and longitudinal coats of muscles on the intestine. The neurons which compose it are the exciters of the parasympathetic outflow through the vagus, and these neurons branch, the two axon fibres having different destinations. A mass of food in the intestine stimulates the muscles above it to contract, and those below it to slacken, thus causing peristaltic action. This is particularly interesting because peristalsis can occur when all the nerves to the intestine are cut, which means that local reflex arcs are formed in Auerbach's plexus. Another plexus (Meissner's), which lies within the muscle-coats of the intestine, has an unknown function.

The effect of impulses travelling out through the para-

sympathetic outflows is to contract the ordinary muscles round the gut, but to slacken the sphincters, to slacken the muscles of the heart and of the blood-vessels near the urethra (causing erection of the penis), to tighten the ciliary muscle and the sphincter of the iris, to slacken the radial muscles of the iris (which allows the pupil to be contracted, and to secrete saliva and tears).
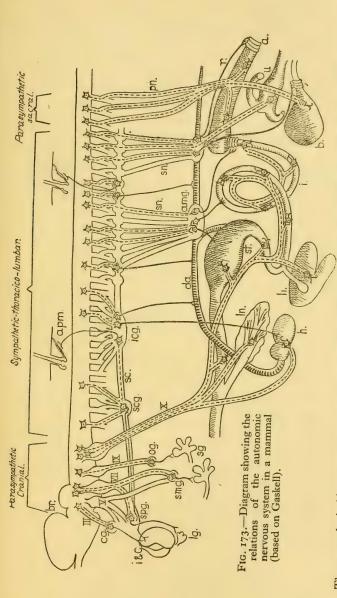
The antagonism between the effects of the sympathetic and parasympathetic systems is remarkable. It may be expressed in the form of a table.

	Ordinary muscles of the gut.	Sphincters of the gut.	Heart.	Radial muscles of the iris.	Sphincter of the iris.
Sympathetic.	Slackens.	Tightens.	Tightens.	Tightens.	Slackens.
Parasympathetic.	Tightens.	Slackens.	Slackens.	Slackens.	Tightens.

It is also interesting to note that the action of the sympathetic system can partly be simulated by the injection of adrenalin, and that of the parasympathetic by injection of acetyl-cholin. The similar effects of adrenalin and the sympathetic are less surprising when it is remembered that the supra-renals and the medulla of the adrenal bodies are derived from cells similar to sympathetic neurons, and which like them have migrated out from the spinal cord.

The case of the gut is particularly interesting, because the ordinary muscles of its coat are antagonistic in their effects to those of the sphincters. It stands to reason, that if the ordinary gut-musculature contracts and propels the contents of the gut along, contraction of the sphincters would prevent this movement of the contents. Now the parasympathetic system tightens the ordinary musculature and slackens the sphincters, and the sympathetic system contracts the sphincters and slackens the ordinary musculature. Further, the cell-bodies of the neurons which tighten the sphincters and slacken the ordinary muscles are in the same ganglion (anterior or posterior mesenteric ganglion, according to the region of the gut). It is possible that it is one and the same neuron which produces two axon fibres, one tightening the sphincters and the other slackening the ordinary muscles. This provides an explanation of how the co-ordination between antagonistic sets of muscles may be brought about.

FIG. 173.—Diagram showing the relations of the autonomic nervous system in a mammal (based on Gaskell).

The sympathetic (thoracico-lumbar) outflow and parasympathetic (cranial and sacral) outflows are indicated. The connector fibres are shown by broken lines, the exciter fibres by full lines. III, oculomotor; V, trigeminal; VII, facial; IX, glossopharyngeal; X, vagus, nerves; a, anus and anal sphincter; amg, anterior mesenteric ganglion; apm, arrector pili muscle; b, bladder; br, brain; cg, ciliary ganglion; da, dorsal aorta; h, heart; i, intestine; i and c, iris and ciliary muscles; icg, posterior cervical sympathetic ganglion; lg, lachrymal gland; lv, liver; ln, lung; og, otic ganglion; pn, pelvic nerve; r, rectum; sc, sympathetic nerve-chain; scg, anterior cervical ganglion; sg, salivary glands; smg, submaxillary ganglion; sn, splanchnic nerves; spg, spheno-palatine ganglion; st, stomach; u, uterus.

No autonomic system is known in Amphioxus. In Petromyzon, neurons are found along the gut, connected with the vagus and probably with " pelvic " nerves. The parasympathetic system is therefore present. The sympathetic system is, on the other hand, not well developed, and imperfectly differentiated from the supra-renal elements. Groups of these cells are found near the spinal nerves and the blood-vessels, but they are not joined together by sympathetic chains. Parallel with this poor development of the sympathetic component of the autonomic system in Petromyzon, it may be mentioned that that animal has no oviduct or bladder, and no smooth muscle under the skin. In the head the eyes are degenerate, and there are no salivary glands, and this is parallel with the absence of differentiated cranial autonomic ganglia. In Selachians, the sympathetic ganglia are joined together by the longitudinal lateral chains, and the ciliary ganglion is present in the head. With the land-vertebrates the full development of the autonomic system appears.

It is not easy to see why the exciter neurons for smooth muscles and glands should migrate out of the central nervous system as they do, and take up positions outside it. It is also very remarkable that some of them should connect with the central nervous system through dorsal nerve-roots (hindbrain outflow of parasympathetic), while others should connect through ventral nerve-roots (midbrain and sacral outflow of parasympathetic and the entire sympathetic). In this connexion it may be noted that in Amphioxus the smooth muscles of the body are innervated through the dorsal nerve-roots, while the ventral roots contain only fibres belonging to the somatic system. The primitive course for fibres innervating smooth muscle, therefore, appears to be through the dorsal nerve-roots, and this primitive feature is retained in the case of the hindbrain (facial, glossopharyngeal and vagus) outflow of the parasympathetic system, but lost in all the rest.

LITERATURE

GASKELL, W. H. The Involuntary Nervous System. Longmans, Green, London, 1920.

LANGLEY, J. N. Autonomic Nervous System. Heffer, London, 1921.

CHAPTER XXXII

THE SENSE-ORGANS

The Eye.—With regard to the eyes, two points of interest present themselves. The first concerns the method of accommodation of the eye for seeing objects at different distances, and the second relates to the capacity of some animals to see a single object with both eyes at the same time.

Accommodation is a simple optical problem concerning the focal length of the lens, the distance of the viewed object, and the distance between the lens and the retina. These three terms must be in relation according to the laws of optics if there is to be a clear image of the object on the retina. The first and the third term are within the animal, and are therefore variable, while the second, the distance of the object, is obviously external to the animal and not under its direct control. It is found that some animals accommodate by altering the distance between the lens and the retina, and others by altering the focal length of the lens itself.

Cyclostomes and Selachians may be left out of account, for their eyes can accommodate but little if at all. In the bony fish, the eye when at rest is accommodated for near vision. This fact is in relation to the optical nature of the medium in which they live, water, through which it is not possible to see very far. The lens is attached to the eye-cup by a retractor lentis muscle, and when this contracts, the lens is brought nearer to the retina, and the eye can then focus objects which are farther away. Land-vertebrates always have their eyes focussed at rest for distant vision, which enables them the earlier to see their prey or their enemies. So, in amphibia, the lens is attached to the eye-cup by a protractor lentis muscle.

By its contraction, the distance between the lens and the retina is increased, and the eye can then focus near objects.

In all the cases so far mentioned, the lens is a rigid body with a fixed and definite focal length, and which has to be moved bodily in order to accommodate the eye. In the remaining vertebrates, the lens is elastic and capable of varying its convexity and focal length. In reptiles, accommodation for near vision is brought about by contraction of the circular muscle of the iris, which has as its effect the increase in convexity of the lens, which thus tends to become spherical. In the birds, there is in addition a striated muscle called Crampton's muscle, contraction of which decreases the diameter of the eyeball in the neighbourhood of the junction between the cornea and the sclerotic. This causes the surface of the cornea to become more convex, and assists the lens to bring rays of light from near objects to a focus on the retina.

The method of accommodation in the mammals differs from that in other vertebrates. The lens is suspended by the suspensory ligament, which is kept tense by the elasticity of the lens trying to revert to the spherical shape. The suspensory ligament is attached to the ciliary process. The ciliary muscle is attached to the cornea in front and to the choroid behind, so that when it contracts, the choroid and ciliary process are brought forwards. This forwards movement of the ciliary process reduces the tension on the suspensory ligament, and the lens is allowed to become more spherical, which increases its refractive power and enables it to accommodate the eye to near objects. The change in focal length of the lens is therefore only indirectly due to the action of the ciliary muscle.

In some vertebrates, and especially those of nocturnal habits, the eyes do not accommodate for distance at all, which fact does not prevent them from enjoying good sight, as does the owl. In daylight, the pupil may be so contracted as to simulate a " pinhole " camera, in which accommodation is unnecessary.

In mammals the ciliary muscle is contracted by impulses passing in fibres of the parasympathetic system through the oculomotor nerve and the ciliary ganglion. Other fibres

following the same path constrict the pupil (contract the sphincter and relax the radial muscles of the iris). The pupil is dilated by impulses in fibres coming from the sympathetic system of the neck.

In the lower vertebrates, the eyes are on each side of the head, and there is little, if any, overlap in the two fields of vision. In these forms, the decussation or crossing-over of the fibres at the optic chiasma is complete : the fibres from an eye run to the opposite side of the brain. In the higher vertebrates, on the other hand, it is common for the fields of vision of the two eyes to overlap considerably, and even to coincide. In these cases both eyes can be brought to bear on a single object, which enables the animal to estimate distance. This is of importance in arboreal animals which have to gauge the strength of their efforts in leaping from branch to branch. This binocular vision is present in the monkeys and man, in the owls, and to a varying extent in other animals.

The possession of binocular vision is a great advantage, but it robs the animal of vision over a large radius around it, which it would have if its eyes diverged widely on each side of the head. It is found as a rule that the more timid mammals have widely divergent axes of vision, amounting to nearly two right angles in the case of the rabbit. The rabbit therefore can see objects almost everywhere all round it ; it uses its eyes qualitatively to warn it of the approach of enemies. The axes of vision of the lion, on the other hand, are almost parallel ; it sacrifices a large field of vision for the advantage of using its eyes quantitatively in estimating distance and spatial relations.

In mammals with binocular vision, it is important that the movements of the two eyes should be co-ordinated so that their axes of vision remain more or less parallel with one another. In other animals each eye can be moved separately, and this faculty is extremely developed in Chamæleo.

The fibres from the eyes of mammals such as the rabbit decussate almost completely at the optic chiasma. In the monkeys and man, on the other hand, the decussation of the fibres is incomplete. Fibres from the lateral portion of the retina of each eye do not cross-over, but go to the same side

of the brain. It is the fibres from the median portions of the retinæ which cross-over and go to the opposite side of the brain. The images of one object fall on corresponding points in the two retinæ, and the fibres from these corresponding points run to one and the same side of the brain.

Many of the lower vertebrates have been shown to be sensitive to different colours. It is supposed that the cones of the retina are sensitive to colour, and that the rods only perceive light and dark. Nocturnal animals such as owls and bats have scarcely any cones, and are presumably colour-blind. The proportion of cones in the retina increases as a rule from the lower to the higher vertebrates. In the higher Primates and in man, the eyes have " corresponding points " of optimum sensitiveness (the macula lutea or " yellow spot "), in which the retina consists of cones only, without any rods.

In some vertebrates the eyes have been lost. They are very degenerate in some of the Cyclostomes, which lead a semi-parasitic life, and in the Urodele Proteus, which inhabits the dark caves of Carniola. Fish which live in the dark of the abyss of the ocean or in caves may be blind and eyeless, as, for example, Ipnops, Amblyopsis, and Lucifuga. Among mammals, the eyes are often reduced in forms which live in the dark in burrows underground. The common mole is an example, and a comparable but even more far-reaching reduction of the eyes has taken place independently in the " marsupial mole " Notoryctes.

The Pineal.—There is no doubt that the early vertebrates were capable of seeing by means of their pineal organs, through the pineal foramen in the roof of the skull, though possibly not of forming an image. Among living forms, Petromyzon has two pineal organs ; other forms have only one, which may represent the original right or left organ. The pineal is least degenerate in Sphenodon. It is in the form of a vesicle of which the upper wall forms the lens and the lower the retina, which is connected by nerve-fibres with the brain. This retina is not " inverted," as is that of the paired eyes. Surrounding the retina is pigment, and the organ is sensitive to light.

In birds and mammals there is no pineal foramen in the skull, and the pineal organ remains beneath the bone.   It is reduced to a solid vestige and its function is changed from that of a visual organ to an organ of internal secretion, or ductless gland.

The Ear.—The most primitive part of the ear is the utricular portion with its semicircular canals and ampullæ. Myxine has one, and Petromyzon has two semicircular canals on each side.   All other Craniates have three, in planes at right angles to each other.   In the ampullæ are the statolithic particles which are supported on sensory cilia.   Gravity makes these particles weigh on the cilia immediately beneath them, whatever the position of the animal, and so the animal is informed of its position with regard to the vertical according as to which of the cilia are so stimulated.   The semicircular canals contain fluid, the endolymph, as do all parts of the auditory sac.   When the animal starts or ceases moving, a flow of endolymph takes place in the semicircular canals, which resolve the direction of the movement into resultants in the three planes of space in which they lie.   While the statoliths are static, the semicircular canals are dynamic organs of balance.

Hearing is the perception of mechanical vibrations of low frequency.   Fish are capable of hearing with their auditory organs, but this sense only becomes important in the vertebrates which have left the water, and are therefore subject to vibrations in air.   This is significant because these animals are also the first to emit vocal sounds.   Since these animals are autostylic and no longer breathe by gills, the spiracular cleft and the hyomandibula are no longer needed to subserve their primitive functions ;   they give rise to the tympanic cavity (and Eustachian tube) and columella auris (stapes) respectively.   The vibrations of air impinge on the tympanic membrane or ear-drum, and are conveyed by the columella auris across the tympanic cavity to the auditory capsule.   The wall of the auditory capsule is imperforate in the fish and in the most primitive Stegocephalia (Eogyrinus).   In the remaining vertebrates the auditory capsule has two openings

in its wall. One of these is the fenestra ovalis which enables the vibrations to be imparted to the fluid (perilymph) which bathes the auditory sac. The other is the fenestra rotunda ; it is covered by a membrane which absorbs the vibrations in the perilymph and so brings them to an end.

That part of the auditory sac which is actually concerned with hearing is the cochlea, rudimentary in amphibia but well developed in the higher vertebrates. The vibrations of the perilymph are imparted to the endolymph within the cochlea, which in its turn stimulates the sensory cells. In mammals where the development of the ear is at its highest, the auditory ossicles are three in number, the cochlea is long and coiled, and an external ear assists in collecting the air vibrations.

Cyclostomes, fish, and larval amphibia possess a system of sense-organs known as the lateral-line organs, and which serve to appreciate vibrations in water of low frequency. The ear itself is to be regarded as a specialised organ of the lateral-line (or " neuromast ") system.

The Nose. — The olfactory organ or nose contains an epithelium which is sensitive to very minute quantities of chemical substances, dissolved or suspended in water, or suspended in air. In Dipnoi and Tetrapods the nose has an open connexion with the mouth cavity, and so enters into the service of the respiratory system, enabling air to reach the lungs without opening the mouth. This connexion does not exist in forms below the Dipnoi (except in Myxine, where the hypophysial sac opens into the gut).

Taste-organs.—The nose is a distance-receptor, appreciating chemical substances from afar. Taste-organs, on the other hand, serve for appreciating substances in contact with the animal, and especially in connexion with the opening of the alimentary canal. Taste is a visceral sense, while smell is a somatic sense. While in most vertebrates the taste-organs are restricted to the mouth, in some fish, such as the catfish, they are distributed over the surface of the body.

Jacobson's Organ.—Associated with the nose in land-vertebrates is a pair of pouches which constitute Jacobson's, or the vomero-nasal organs. Their function is doubtful, but

it is probably concerned with smelling the food in the mouth, with which they are in communication. In some forms, including man, Jacobson's organs disappear. In the snakes they are very highly developed, and the tips of the forked tongue enter their openings in the roof of the mouth. Substances gathered on the tongue when protruded are thus placed in contact with the sense-organ.

LITERATURE

VON BUDDENBROCK, W. Grundriss der vergleichenden Physiologie. Vol. 1. Borntraeger, Berlin, 1924.

HERRICK, C. JUDSON. An Introduction to Neurology. Saunders Co., Philadelphia and London, 1922.

CHAPTER XXXIII

THE DUCTLESS GLANDS

THE ductless glands, or endocrine organs, are a group of structures remarkable no less for their function than for their mode of development, and their evolutionary history. The method of pouring out a secretion into the blood-stream instead of leading it away by a duct, is secondary, and some glands which are now ductless doubtless possessed ducts at earlier stages in evolution. Others, comprising the majority of the endocrine organs, were originally not glands at all, but structures which have become useless in the sense that their original function is not or cannot any longer be performed. They have become modified and their functions have changed in a remarkable manner. It is perhaps not without significance that so many of the ductless glands should have such a history of structural and functional transformation. Another peculiarity which applies to several at least of these organs is that in development they arise from two separate rudiments, distinct in manner and place of origin, and even in the germ-layer from which they are formed.

The method of secreting into the blood-stream carries with it a property which cannot be possessed by glands secreting by means of definite ducts, for the latter can only communicate with definite and restricted spaces in the body, and the effects of such secretions must be only local. On the other hand, the blood circulates all over the body, carrying the endocrine secretions with it. These can therefore affect the body as a whole, and they are of immense importance both during development and during adult life in effecting correlations of the various parts with one another. The ductless glands act

as a chemical mechanism of integration relying on the transportation of the stimulus (the secretions) through the vascular system; and this mechanism is complementary to that of nervous correlation and integration which involves not transportation of stimuli but conduction of impulses arising from stimuli along special paths, the nerves. " Secretin," which is produced by the lining of the intestine and stimulates the pancreas to secrete, has been mentioned in Chapter XXVI.

The Thyroid.—The thyroid was originally a longitudinal tract of ciliated and mucous-producing cells on the floor of the pharynx, called the endostyle. The endostyle is typically represented in Amphioxus (and in the Ascidians), where it is correlated with the ciliary method of feeding, and serves to make a moving " fly paper," on to which particles of food adhere and get carried safely back into the intestine (along the hyperpharyngeal groove), instead of getting carried out through the gill-slits by the outgoing current of water and lost. Such an endostyle is also present in the Ammocœte larva of Petromyzon. In the adult, however, it becomes closed off from the pharynx and sunk beneath it, and it gives rise to the vesicles of the thyroid. In all Gnathostomes the thyroid arises in development from the floor of the pharynx, and in some Selachii its cells still show traces of flagella. In the bony fish, the thyroid is not enclosed in a capsule of connective tissue, with the result that when it undergoes abnormal growth (goitre) it may become carcinomatous and give rise to a malignant cancer which invades the neighbouring tissues, including the bones. In the higher forms the thyroid is enclosed in a capsule.

The secretion of the thyroid increases the speed of the processes of metabolism in the body, and it has been said that it stands in the same relation to the body as the draught does to the fire. It plays an important part in the metamorphosis of amphibia, by promoting the growth of the (previously invisibly determined) regions into the organs which distinguish the tadpole from the adult frog or newt.

The Pituitary.—In all Craniates, the pituitary body is a composite organ formed from the hypophysis which grows in

from the superficial ectoderm of the front of the head, and the infundibulum which is a down-growth from the floor of the forebrain. In Myxine these two constituents remain separated by connective tissue, but in all the remaining animals they are intimately connected and fused. In the Tetrapods it is possible to distinguish four parts in the pituitary, of which three (the anterior, intermedia, and tuberalis) arise from the hypophysis, and one (the nervosa) arises from the infundibulum. The intermedia is always (except in Myxine) plastered on to the nervosa, and the two together form the neuro-intermediate lobe. This is separated from an anterior lobe (formed of the anterior part) by the hypophysial cleft which represents the original cavity of the hypophysial ingrowth, Rathke's pocket.
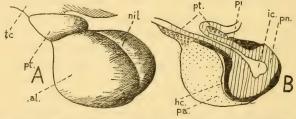
FIG. 174.—The pituitary body of a cat, seen, A, from the left side ; B, in longitudinal section.

al, anterior lobe ; *hc*, hypophysial cleft ; *ic*, infundibular cavity ; *nil*, neuro-intermediate lobe ; *pa*, pars anterior ; *pi*, pars intermedia ; *pn*, pars nervosa ; *pt*, pars tuberalis ; *tc*, floor of the brain.

In some animals, the hypophysial cleft becomes obliterated in the adult.

In evolution, the hypophysis appeared before the infundibulum, for in Amphioxus the latter is not represented, whereas the hypophysis is present in the form of the preoral pit. The preoral pit communicates with the (left) anterior head-cavity just as the hypophysis communicates with the premandibular somite in a number of Craniates. In the adult Amphioxus the preoral pit becomes absorbed in the oral hood and gives rise to the ciliated organ which produces a current of water towards the mouth. Thereafter it probably sank into the tissues and became a gland secreting by a duct into the mouth. This duct (which represents the open mouth of the cavity of

Rathke's pocket) is preserved in Polypterus, and Cyclostomes. In the latter, however, the duct has given rise to the large hypophysial sac which extends beneath the brain and has lost contact with the pituitary body. At the next stage in its evolution it must be imagined that the gland entered into relations with the infundibulum of the brain, and that it adopted the method of secreting into the blood-stream.

The functions of the pituitary are many, and they are only very imperfectly known. It must suffice to say that among these functions are those of : promotion of growth, control of blood-pressure, causing contractions of the uterus, expanding the black pigment-cells in the skin of amphibia, and stimulating the mammary glands to secrete milk.

The Adrenal.—Like the pituitary, the adrenal bodies of the Tetrapods are composite structures. They are made up of an external cortex derived from the (mesodermal) cœlomic epithelium, and a central medulla (chromaffine tissue, so-called from its staining reactions) derived from the (ectodermal) cells which have migrated out from the nerve-tube in connexion with the sympathetic nerve-cells. In the fish, these two components are quite separate. The cortex of the adrenal is in them represented by the inter-renal, which, as its name implies, is situated between the kidneys. The medulla is represented by a number of supra-renal bodies which lie on or near the sympathetic nerve-chains, on each side of the aorta ; they are roughly segmental in arrangement. In the Cyclostomes, the supra-renals are closely associated with the ganglia of the dorsal roots, but the inter-renals are not well known.

Coming to the Tetrapods, the inter-renals and supra-renals are fused together to form the adrenal bodies, but in the more primitive forms such as the newts, these still resemble the fish in that they are not compact but form separate strips extending along the sympathetic nerve-chains, from the kidney to the anterior region of the thorax. The carotid gland, which is situated at the joint of the internal and external carotid arteries, is one of these.

The secretion of the medullary portion of the adrenal

2 D

(adrenalin) has been synthetically prepared, but in spite of this fact, little is known of the functions of the gland, except that it produces effects similar to those due to stimulation through the sympathetic autonomic nervous system.

The Thymus.—The thymus first appears in the fish as a series of paired upgrowths from the roof of the gill-slits. In the Selachians it is more or less segmental in its arrangement, but in higher forms the correspondence is lost, and the number of slits which contribute to it is reduced. It controls the formation of the shell, shell-membranes, and albumen in birds' eggs.

The Parathyroid. — The name parathyroid is given to bodies which are usually situated close to or even in the thyroid, but which differ from the latter in their structure and method of development. They arise from the ventral regions of the 3rd and 4th visceral pouches in the Tetrapods, and are apparently absent in the fish.

The Pineal.—The pineal eye has already been described in connexion with the sense organs. In the higher vertebrates this structure degenerates and is transformed into a gland.

The Pancreas.—In addition to its function of producing enzymes for the purpose of digesting the food in the intestine, whither the enzymes are conducted by the pancreatic duct, the pancreas also functions as an organ of internal secretion. The tissue responsible for producing this internal secretion is that known as the islets of Langerhans, and its production is called insulin. The function of insulin is to store up glycogen in the liver, in which respect it is antagonised by the adrenalin. Diabetes is the result of faulty or non-functioning of the islets of Langerhans. In some Teleost fish, the endocrine islet-tissue may form little masses separate and apart from the ordinary pancreatic tissue, which secretes the digestive pancreatic juice.

The " Puberty " Gland.—The reproductive glands, ovary and testis, in the birds and mammals produce internal secretions which are concerned with the development and maintenance of the characters which distinguish one sex from the other. Since these secretions are essential for the proper sexual

differentiation of the developing animals, the glands producing them have been called " puberty " glands.

The Corpus Luteum.—The corpus luteum is the name given to what is really a temporary endocrine organ in the mammals. After an egg has vacated its Graafian follicle, the follicle undergoes changes resulting in the increase in size of the follicular cells, and the invasion of the follicle by connective tissue and blood-vessels. Should the egg liberated not get fertilised, the corpus luteum soon disappears. Should fertilisation result, however, and the blastocyst become attached to the wall of the uterus, the corpus luteum persists and increases in size, until the end of pregnancy. During this time it produces a secretion the functions of which are to prevent other eggs from being released from the ovary, and to control the growth of the uterus and the secretion of milk.

<div align="center">LITERATURE</div>

RIDDLE, O. Internal Secretions in Evolution and Reproduction. The Scientific Monthly, vol. 26, 1928.
SWALE VINCENT. Internal Secretion and the Ductless Glands. Arnold, London, 1924.

CHAPTER XXXIV

REGULATORY MECHANISMS

ALL animals below the birds and mammals are what is usually called " cold-blooded," or poikilothermous. Actually, these animals are not so much cold as dependent on the environmental temperature, which may be hot. It is a mistake to regard " cold-blooded " animals as necessarily cold, lethargic and sluggish, for in a tropical climate their temperature is high and they may be very active. Nevertheless, since the processes of life can only go on within a certain limited range of temperature, the fact that an animal is dependent on its environment for its temperature necessarily restricts the kinds of environments in which it is capable of living. Further, within the suitable habitat, the degree of activity of the animal will depend on the temperature. This inconstancy of thermal conditions is a serious bar to the further evolutionary progress of the poikilothermous animals.

The advantage which the birds and mammals have in being " warm-blooded " (homothermous) is not only the fact that the temperature at which their biological processes go on is high, but still more the fact that this temperature is constantly maintained, regardless of the temperature of the environment.

The processes of metabolism, and especially muscular activity, entail the production of heat. Some warm-blooded animals shiver when they are cold, and their muscles are then thrown into series of contractions. There is therefore a source of heat within the organism which tends to make the temperature rise. At the same time, heat is continually being lost by radiation from the surface of the animal. The maintenance of a constant temperature within the animal therefore depends

on a regulation and balance of the amounts of heat produced
and lost. Poikilothermous animals have a temperature only
slightly higher than that of the environment. Some seem
to be able to raise their temperature slightly for a period by
muscular contractions, such as the python when it is coiled
round its eggs. But these animals have no means of combating
really cold external temperatures, during which they must
either hibernate or die. Within limits, the hotter the tempera-
ture, the better are the conditions for poikilothermous forms.
Some lizards, however (Varanus, Uromastix), when exposed
to great heat, increase their rate of breathing very considerably,
and so resort to panting. Panting results in the lungs getting
rid of large quantities of water vapour, and as heat is absorbed
in the conversion of water into vapour, panting means loss of
heat also. Uromastix, which inhabits deserts, is dark in colour
up to a temperature of $41°$ C., but as the temperature rises
above this point, it tends to become white. Since dark colours
absorb heat and light colours reflect it, Uromastix has a peculiar
mechanism which tends roughly to regulate its intake of heat
from the environment. This method, however, is quite
different from that of homothermous animals, birds, and
mammals. In the first place, the homothermous animals have
an external covering which is a bad conductor of heat ; this
takes the form of feathers in birds, hairs in terrestrial mammals,
and oil or blubber in birds and mammals which lead an aquatic
existence. The effect of such a layer is to minimise the loss
of heat by radiation. Next, they have more efficient respiratory
and vascular systems, notably a four-chambered heart with
complete separation of the arterial and venous circulations.
In the Monotreme Echidna, the temperature is regulated by
varying the amount of heat produced, but it has no method of
varying the amount of heat which it loses. It has no sweat-
glands, no increase in the amount of blood in the skin (vaso-
dilatation), and it does not resort to panting. The heat-
production of Echidna varies according to the difference
between its temperature and that of the environment. How-
ever, this regulation is not very efficient, for if the environ-
mental temperature varies from $35°$ to $5°$ C., the temperature

of the animal will vary by about 10° C. Not only is the constancy of the temperature less than that of higher mammals, but the actual normal internal temperature is lower, being about 30° C. In cold weather, Echidna hibernates. Its protective covering of hair is poor, and, like a few other mammals (such as the marmot), it becomes almost poikilothermous. On the other hand, in hot weather when the temperature rises above 35° C., Echidna dies of apoplexy (unless it is æstivating, deep beneath the ground), for its only method of countering a rise in the environmental temperature is to reduce its own internal heat-production, and a point is reached below which it cannot reduce its metabolism and still live.

The other Monotreme, Ornithorhynchus, has a slightly higher normal temperature, 32° C., and it keeps it a little more constant. Not only can it vary its heat-production, but it can also vary its loss of heat by means of evaporation of water from its sweat-glands.

The higher mammals regulate their temperature almost entirely by controlling the heat-loss. This they do by three methods : by the evaporation of water from the sweat-glands, by the dilatation of the blood-vessels in the skin, and by the acceleration of respiration or " panting." The heat-production in these animals is not increased unless the external temperature drops considerably. The Marsupials are intermediate between the Monotremes and the higher mammals in the efficiency of their temperature-regulations.

In birds, heat is lost by evaporation of water through the lungs and air-sacs.

The advantages accruing from the possession of a high and constant internal temperature are very great. Not only does it allow of a higher rate of living, since chemical reactions are accelerated at high temperatures, but it enables differentiations and specialisations to arise which would be wrecked if the speed of the metabolic processes (or in other words, the internal temperature) were not constant. Further, it enables the animals to inhabit climates in which poikilothermous forms either cannot live, or have to spend considerable time hiber-

nating against the cold or æstivating against the heat. So it is found that the supreme and dominant animals in arctic regions are the birds and mammals, while in the tropics, reptiles can compete successfully with birds and mammals.

It is interesting to notice that during most of the period of incubation, the embryo chick is poikilothermous. It is only shortly before hatching that it acquires the capacity of maintaining a uniform temperature. The same is true of new-born mice, which become homothermous by the tenth day after birth.

Another matter for which a regulatory mechanism has been evolved in the vertebrates is the osmotic pressure of the blood. Of aquatic invertebrates it may in general be said that their body-fluids have roughly the same osmotic pressure and the same percentage of salts as the water in which they live, and that these vary as the water varies. It is interesting to find that in the Selachii, the osmotic pressure of the blood is not constant either, but varies with the water. The salts in the blood are only about half as concentrated as in sea water, but the blood of Selachians contains urea, which makes up the difference. In the Teleosts, the osmotic pressure of the blood is about one-third that of sea water, but it is kept more or less constant. This regulation is more efficient in some forms than in others ; the osmotic pressure varies with that of the surrounding water slightly in the cod, varies more in the plaice, and varies still more in the eel, which alternates between fresh and sea-water. As a rule the osmotic pressure of the blood of fresh-water Teleosts is lower than that of the marine forms.

In the land-vertebrates, the osmotic pressure of the blood is kept constant, and regulated by the kidneys, in spite of variations in food and drink.

In an animal like a Selachian, living in the sea, it is not of much importance if water and salts be lost from the body, as they can be replenished from the medium in which it lives. In a land-vertebrate the case is different, and the loss of water and salts is regulated. The importance of maintaining a constant osmotic pressure of the blood lies in the fact that it entails constancy in the concentration of salts, or in other words,

a stable " internal environment " ; and stability of conditions is essential for highly specialised and co-ordinated processes of life.

The relation between the quantities of oxygen and CO_2 in the blood is regulated by the respiratory system, controlled by a centre in the brain. If the blood is rich in CO_2 the respiratory movements are accelerated, and conversely they are retarded if the quantity of CO_2 is low. In this connexion it must be remembered that the respiratory movements of the fish and amphibia are effected by the muscles of the visceral arches. These are visceral muscles, innervated by visceral efferent fibres in the dorsal cranial nerve-roots, and the centre which controls them is in the visceral sensory lobe of the medulla oblongata. In the Selachian (Raia) it is perhaps better to speak of several centres, one corresponding to each of the 7th, 9th, and 10th cranial nerves. Each of these segmental centres in Raia has a degree of autonomy of its own, for if separated from the others by cutting across the medulla, it continues to regulate the muscular movements in the visceral arch or arches to which it is connected.

In the amniotes, however, the respiratory movements are effected by the intercostal muscles (moving the ribs) and the muscles of the diaphragm. These are somatic (myotomic) muscles innervated by somatic efferent fibres through ventral nerve-roots in the region of the neck and trunk. Nevertheless, the " respiratory centre " is still in the medulla oblongata, in the primitive position which it occupied in the fish and amphibia, but it no longer shows the simple segmental arrangement.

Lastly, attention may be paid to two features which the higher vertebrates possess, and which though not strictly regulatory (compensating) mechanisms, nevertheless serve to ensure maximum constancy of conditions. The first of these is concerned with the fact that the ovary and testis in birds and mammals serve not only for the production of reproductive cells, but they also furnish a chemical secretion which evokes and maintains the development of the secondary sexual characters.

The other feature refers to the method of ossification of certain cartilage-bones by means of a diaphysis and two epiphyses, which is characteristic of the mammals. This method enables the bones in question to function as supports and hinges, and at the same time to grow and enlarge so long as the diaphysis and the epiphyses remain separated by cartilage. But once the diaphysis becomes firmly united by bone with the epiphysis at each end of it, the growth of the bone as a whole ceases. The maximum size of such bones is therefore limited, as is that of the animal. In several respects, therefore, the higher vertebrates differ from the lower. With the temperature, the osmotic pressure and the acid-base relations of the blood regulated and constant, the higher vertebrates are largely independent of the environment. Indeed, they have a constant internal climate and " environment " of their own, in which they live sheltered from external agencies, with, in mammals, a constant final adult size.

The possession of this " internal environment " is not only one of the chief means of survival of the higher vertebrates, but it has also enabled them to become as specialised and perfected as they are.

LITERATURE

DAKIN, W. J. The Osmotic Concentration of the Blood of Fishes taken from Sea Water of naturally varying Concentration, and Variations in the Osmotic Concentration of the Blood and Cœlomic Fluids of Aquatic Animals, caused by Changes in the External Medium. Biochemical Journal, vol. 3, 1908.

HALDANE, J. S. Respiration. Yale University Press, 1922.

HIDE, I. H. Localisation of the Respiratory Centre in the Skate. American Journal of Physiology, vol. 10, 1904.

KREHL, L., und SOETBEER, F. Untersuchungen über die Wärmeökonomie der Poikilothermen Wirbeltiere. Pflüger's Archiv. f. d. Gesammte Physiologie, vol. 77, 1899.

MARTIN, C. J. Thermal Adjustments and Regulatory Exchange in Monotremes and Marsupials. Philosophical Transactions of the Royal Society, Ser. B, vol. 195, 1903.

SCOTT, G. G. A Physiological Study of the Changes in Mustelus Canis produced by Modifications in the Molecular Concentration of the External Medium. Annals of the New York Academy of Science, vol. 23, 1913.

CHAPTER XXXV

BLOOD RELATIONSHIPS AMONG THE CHORDATES

THE various species of animals differ not only in their structure, their method of development and their habits, but also in the chemical composition of their tissues. The most useful tissue to take in this connexion is the blood. Now, chemical methods are not sufficiently refined to detect the difference between the bloods of two animals and to estimate the degree of similarity which they show. It is possible, however, to have recourse to biological methods by making use of the property which animals possess of developing immunity. If horse's blood, for example, is injected into the vascular system of a rabbit, the rabbit will after a time produce a substance in its blood which reacts to horse's blood, and precipitates it. This is the same principle as that used for preparing antitoxins for certain diseases. As to how the antitoxin or antiserum is produced, little is known, but it suffices for present purposes to realise that in the hypo-thetical case just described, rabbit's blood immunised against horse's blood will always precipitate horse's blood, to the extent of 100 per cent. This means that anti-horse serum, as it may be called, is specific against horse, and it is a matter of no importance what kind of animal has been used to produce the antiserum. But the specificity against horse is not quite complete. Anti-horse serum, as it may be called, will produce no effect whatever if mixed with, say, blood of a bird ; but it will produce a slight precipitation with blood of pig, and still more with blood of ass. This means that the blood of horse is more similar to that of ass than to that of pig, as regards its chemical composition, and this is just what would be expected

from a knowledge of the comparative anatomy and embryology, and from the palæontology regarding these three species.

The precipitin blood-tests therefore furnish a means for estimating the relative similarities between the bloods of different animals, and they are not only a biochemical proof of the theory of evolution, but also an index for classification.

The following are a few tables showing the relative affinities between the bloods of a number of vertebrates : *

Anti-human serum, mixed with blood of :—

Man	gives		100 per cent. precipitation.	
Gorilla	,,	64	,,	,,
Orang Outang	,,	42	,,	,,
Baboon	,,	29	,,	,,
Ox	,,	10	,,	,,
Sheep	,,	10	,,	,,
Deer	,,	7	,,	,,
Horse	,,	2	,,	,,
Marsupial	,,	0	,,	,,

These results show several interesting points. In the first place, the great similarity between the blood of man and that of the gorilla should dispel any doubt (should any be left) concerning the evolution of man from lower mammals. The precipitation percentages show that human blood is more like that of the apes than that of the baboon, and more like the latter than the blood of animals like horse and deer. This fits in perfectly with evidence derived from other sources. It is also interesting to note that two animals which are believed to be closely related to one another like ox and sheep, should show the same degree of dissimilarity to man. The relationship between sheep and ox can also be tested by immunising a rabbit to sheep blood.

Anti-sheep serum mixed with blood of :—

Sheep	gives		100 per cent. precipitation.	
Ox	,,	75	,,	,,
Antelope	,,	67	,,	,,
Reindeer	,,	35	,,	,,

The relationship between sheep and ox is here definitely shown to be close.

* From Nuttall.

Some of the most interesting results are those which refer to the relative affinities between the various groups of reptiles, and between them and the birds.

Anti-fowl egg serum mixed with blood of :—

Crocodile, gave a positive result (precipitation) in 50 per cent. of cases.

Chelonian	,,	,,	,,	,,	40	,,	,,
Lacertilian	,,	,,	,,	,,	7	,,	,,
Ophidian	,,	,,	,,	,,	6	,,	,,

These results show that the reptiles (alive now) nearest akin to the birds are the crocodiles, which again corroborates all the evidence from other sources. It further indicates that the crocodiles and turtles are more closely akin to one another than they are to the lizards and snakes, which, again, are fairly closely allied to one another. This is further shown by the following :—

Anti-chelonian serum mixed with blood of :—

Chelonian gave a positive result in 87 per cent. of cases.

Crocodile	,,	,,	,,	25	,,	,,
Lacertilian	,,	,,	,,	0	,,	,,
Ophidian	,,	,,	,,	6	,,	,,

Besides the precipitin tests, there are other methods of estimating the blood-relationships of vertebrates. For one thing, it is found that blood of any particular species has the power of destroying the blood-corpuscles of other species, to an extent varying with the remoteness of the relationship between them. Again, it is found that the degree of virulence with which an animal will suffer from a human disease varies with its degree of kinship to man. So syphilis attacks the chimpanzee more seriously than the orang, and the latter more than the baboon. Lastly, attention may be called to the so-called blood-groups, into which the human race is divided. There are four of these blood-groups, and they are due to two agglutinating substances, which may be absent, or one, or the other, or both may be present, in the blood of a man, and cause clotting when the blood is mixed with that of another incompatible group. Incidentally these groups are further interesting in that there is reason to believe that they are inherited by means of Mendelian factors, but their main

interest from the present point of view lies in the fact that the blood-groups and agglutinating substances are also found in monkeys. Here, therefore, are definite biochemical characters which are shared by monkeys and man, and which were derived from a common ancestor.

LITERATURE

LANDSTEINER, K., and MILLER, C. P. Serological Studies on the Blood of the Primates. Journal of Experimental Medicine, vol. 42, 1925.

NUTTALL, G. H. F. Blood Immunity and Blood Relationship. Cambridge University Press, 1904.

PART IV

EVOLUTIONARY MORPHOLOGY

CHAPTER XXXVI

THE BEARING OF PHYSICAL AND CLIMATIC FACTORS ON CHORDATES

To understand their evolution and life it is essential to consider animals in relation to their environment. During the time since chordate animals first appeared, the environment has changed very considerably at one time or another. Of the most primitive forms there is no record preserved, for the simple reason that these animals did not possess structures capable of preservation by fossilisation. The earliest known vertebrates are from the Silurian period, and they were fish. The earth was at this time covered with shallow seas containing coral-reefs which are indicative of a mild climate. In the ensuing Devonian period, shallow lagoons and enclosed basins were in abundance, and the land which had emerged enjoyed desert conditions with little rainfall. It is towards the end of this period that the first land-vertebrates (Stegocephalian amphibia) appeared. The next or Carboniferous period was one of tropical climates, during which luxuriant forests covered the land. The trees had no rings of growth, which fact proves that there were no seasons. True reptiles first appeared here. In the late Carboniferous and Permian period the climate became colder as the continents rose and mountain chains were formed, resulting in an ice-age or glacial period. In the following Trias, warm conditions returned, without seasonal variation. The earliest known mammals belong to this period. Warm conditions persisted throughout the Jurassic period, in which the first birds are found, but this period is pre-eminently

the " age of reptiles," not only on account of the number of different types which flourished, but also because of the gigantic size to which many of them grew.

In the Cretaceous, cold conditions returned with seasonal variations. Mountain-building and glaciation occurred in some parts of the earth, the temperature of which was now considerably reduced. At this time and perhaps for this reason the majority of the reptiles which had hitherto been so successful, went extinct and were superseded by mammals as the dominant animals. After this time, hot conditions set in again for the main part of the Tertiary era, gradually diminishing towards its close when a fresh bout of mountain-building erected the Alps. Then followed the great Ice-Age. Mammals continued evolving during this period, towards the end of which man appeared.

The most important changes in the environment as far as the vertebrates were concerned were the drying-up of the lagoons and estuaries in the Devonian, and the variations of temperature.

It is a characteristic feature of desiccated areas that the water expanses which they possess shrink to ponds, and the oxygen-content of the water decreases owing to the quantities of decomposing organic matter with which the ponds become filled. Under such circumstances it is obvious that fish which are provided with means of supplementing their branchial respiration would have a much greater chance of surviving, and the first step in this direction was the habit of taking air into the pharynx when at the surface. At the present day, inhabitants of such waters show diverse adaptations, but by far the most important of these from the present point of view are the Dipnoi, with their lungs. There is little doubt that the ancestors of the Tetrapods encountered and mastered conditions of desiccation in fresh water, in the same way as the modern Dipnoi. There is the further danger that under these circumstances the water may dry up altogether, as it does in the case of the swamps in which Protopterus lives, and then the possession of a means for pulmonary respiration is the only condition for survival.

Temperature may vary in several different ways, either in space or in time, or in both. So the tropics and the temperate and polar regions differ in temperature, as do day and night or summer and winter.

Homothermous animals are largely independent of temperature variation in the outer environment since they live in a constant internal environment of their own. However, the outer environmental temperature has a bearing on their size. This follows readily from a consideration of the ratios of surface to volume at different sizes. The surface increases as the square, but the volume increases as the cube of the linear dimensions, so that there is *relatively* more surface in small animals than in large ones. The importance of this for homothermous animals is that the amount of internal heat produced (by metabolism) and lost (by radiation) varies relatively with the surface. So, of two dogs weighing 20 and $3\frac{1}{4}$ kg. respectively, the former will have a surface of 7,500 sq. cm., the latter 2,423 sq. cm. For every kg. of dog, there is in the large dog 375 sq. cm., and in the small one 757 sq. cm. of surface, and the amount of heat given off from the dogs per kg. is twice as high in the case of the small dog as in the case of the large one.

Small homothermous animals therefore radiate *relatively* more heat from their surface than large animals, and this heat-loss has to be compensated by relatively more active metabolism and intake of food. In spite of the fact that mammals and birds grind their food up small (in the mouth in mammals : in birds, in the gizzard) so that the processes of digestion are accelerated, a stage of smallness is reached when the animals have to spend all their time feeding. Shrews and humming-birds are of about this size. If they were smaller than this they would need to consume quantities of food which they would not have time to eat. Especially true is this of regions in which because of seasonal variation the days are short for a period in each year. The ratio of surface to volume therefore establishes a minimum limit of size for homothermous animals in a given outer environmental temperature.

In cold climates, such as prevail in polar regions, homo-

thermous animals tend to be large. They profit by their relatively small surface from which they lose heat, and also by the fact that they do not require to spend all their daylight eating as they would if their surface/volume ratios were large and they were small in size. On the other hand, tropical homothermous animals can afford to be small and to have large surface/volume ratios. The intensity of heat radiation is less than in polar regions because of the higher temperature of the air, and small size enables them to get rid of their heat. Also, there is ample food, and daylight to eat it in, to make up for the heat lost. Homothermous animals as small as humming-birds could not live in really cold climates.

It is worth noticing that fat, which is a poor conductor of heat, forms a layer underlying the skin in the animals inhabiting polar regions (seal, penguin), and so assists in minimising the amount of heat lost by radiation. When, on the other hand, fat is stored by homothermous animals living in hot climates, it is not distributed under the skin all over the body, where it would interfere with heat-radiation, but it is localised and forms humps as in the camel or the zebu.

Whereas homothermous animals tend to be large in polar regions and small in the tropics, poikilothermous animals show precisely the opposite tendency, and for the same reasons. The reptile depends on the outer environment for its heat. In cold climates, when it is not hibernating, it is to its advantage to absorb as much as possible of what heat there is. This is assisted by a large surface/volume ratio, and consequently a small size. Effectively, it is found that the fish, amphibia, and reptiles inhabiting cold climates are smaller than their relatives living under warmer conditions. For in tropical climates, these animals can afford to be large. The giant frogs, turtles, lizards, snakes, and crocodiles of the tropics illustrate this point well. The huge size of the reptiles in the Jurassic period must have been made possible by the hot conditions which prevailed then.

It is further to be noticed that in tropical regions, the poikilothermous animals can compete successfully with the homothermous ; whereas in polar regions, the homothermous

animals dominate over the poikilothermous by reason of their constant internal temperature.   It follows that if a region of high temperature, populated by poikilothermous and homo-thermous animals, were to undergo a reduction of temperature (as by greater elevation of the land above sea-level or the approach of an ice-age), the homothermous animals would survive, whereas the poikilothermous forms would be very likely to go extinct, especially if they were of large size.   This may be what happened at the cold end of the warm secondary era (Trias to Cretaceous inclusive, the " age of reptiles "), when the reptiles all but went extinct, and were only survived by the present-day forms, which furnish a miserable sample of former richness of the reptilian fauna.   At the same time, the homothermous birds and mammals survived, the latter to become the dominant animals.

It is seen, therefore, that certain of the greatest episodes in the history of the vertebrates, such as the evolution of the amphibia, may have been largely conditioned by climatic changes in the earth's crust.   Other episodes were probably related to adaptations to more fixed climatic conditions.   Of these, two only will be mentioned here.   The first concerns the evolution of the early fish.   The original ancestors of the chordates must have been marine forms, but there are certain considerations which suggest that the evolution of the early chordates took place in fresh or estuarine water.   The typical chordate method of locomotion by undulations of the body from side to side may be regarded as an adaptation to life in rivers in which there is a more or less constant flow of water in a certain direction.

The other episode concerns the evolution of man, part of whose ancestral history is related to the habit of living in trees.   It is common for arboreal animals to retain unspecialised limbs, and to acquire the capacity of opposing one or more digits to the others, and so be able to grasp branches firmly.   At the same time the sense of smell becomes less important, while that of sight becomes dominant, leading to binocular and stereoscopic vision, and the capacity to estimate distance.   This is of importance to an arboreal animal in estimating the strength

of its leaps from branch to branch.   The neurological changes which accompany these anatomical ones are the subordination of the olfactory cortex of the cerebral hemisphere (hippocampus) and the elevation of the non-olfactory cortex or neopallium to a dominant position.   In other words, arboreal life favoured the development and evolution of the brain, which is the organ which most distinguishes the Primates, and especially man, from the remainder.

In previous paragraphs it was shown how the minimum limit of size of homothermous animals was determined, and it was found to be affected by the climatic temperature.   The minimum size of poikilothermous Tetrapods has no relation to temperature, but is determined by the capacity of the muscles to actuate the skeleton and move the animal about.

The maximum size of land-vertebrates is limited by the ratio between the weight of the body and the supporting strength of the legs.   The weight varies with the volume which is proportional to the cube of the linear dimensions of the animal.   But the strength of the legs is measured by the cross-sectional area, which is proportional to the square only of the linear dimensions.   The larger the animal is, therefore, the relatively heavier will the load be which the legs have to carry.   If the length of a rabbit is 10 times more than that of a mouse, the weight which the rabbit's legs carry is 1000 times greater than that which the legs of the mouse support.   Against this, the cross-sectional area of the rabbit's leg is 100 times that of the leg of the mouse.   The result is that the weight per square millimetre on the legs of the rabbit is 10 times more than that on the legs of the mouse.   As the strength of the skeletal material (bone) cannot be increased, a stage is reached at which the legs can no longer safely carry the weight of the body, or they must be so large as to be almost immovable. Already in the elephants they are like pillars, and these animals are near the maximum size for land-vertebrates.   For aquatic forms, the conditions are of course different, since by Archimedes' principle the buoyancy of the water reduces the relative weight of the animal, which is usually not borne on the limbs at all.   So the whales and sharks can reach sizes which are

impossible for land forms.   For this reason, it is likely that the largest of the Dinosaurs were more or less aquatic.

LITERATURE

BROOKS, C. E. P.   Climate through the Ages.   Benn, London, 1926.

D'ARCY THOMPSON.   Growth and Form.   Cambridge University Press, 1917.

HALDANE, J. B. S.   Possible Worlds.   Chatto and Windus, London, 1927.

HESSE, R.   Tiergeographie auf ökologischer Grundlage.   Fischer, Jena, 1924.

PRZIBRAM, H.   Form und Formel im Tierreiche.   Deuticke, Leipzig and Wien, 1922.

CHAPTER XXXVII

THE ORIGIN OF CHORDATES, AND THEIR RADIATION AS AQUATIC ANIMALS

FROM studies on all the groups of chordates and comparisons between them, it is possible to arrive at an idea as to what the original chordates must have been like. They were small, bilaterally symmetrical, and no part of them was sufficiently hard or resistant to be capable of preservation by fossilisation. They were marine animals, as are their lowest representatives at the present day. Some of these may now be considered, for, although they are specialised often to the point of degeneracy, and are of no use in the interpretation of the higher chordates, they show some characters which assist in estimations of the relations which the chordates bear to other animals.
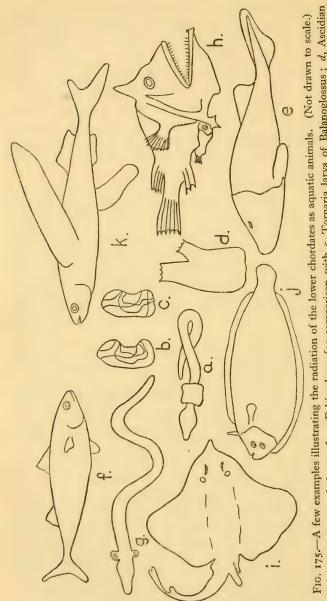
Balanoglossus is a " worm-like " form, with the following chordate features : gill-slits, ciliated grooves assisting in the process of feeding, a dorsal nerve-cord which for a short portion of its length is tubular, and a skeletal structure in the anterior region of the body which is held to represent a rudimentary notochord. From the latter possession it is classed as a Hemichordate. The body is divided into three regions, " proboscis," " collar," and " trunk," and is adapted to its mode of life, which is burrowing in the sand. Its chordate affinities are obvious from the characters just mentioned, but other features ally it to a number of invertebrates, and especially the Echinodermata. The free-swimming larval form of Balanoglossus, the Tornaria, is very similar indeed to the larval forms of the Echinoderms, in general form, in the arrangements of the bands of cilia which it carries, and in the method of origin of the mesoderm. The latter arises as three

pairs of pouches from the archenteron (strictly, two pairs and an anterior median pouch which represents a fused pair). Such cœlomic sacs are enterocœlic, like the anterior gut-diverticula of Amphioxus. The three sets of cœlomic pouches persist in the adult Balanoglossus, and it is interesting to notice that the first two sets, forming the cavities of the " proboscis " and of the " collar," have openings to the exterior. These openings are cœlomostomes, comparable to the water-pores of the Echinoderms, and the connexions which are occasionally found in Craniates between the premandibular somites and the hypophysis (" proboscis-pores ").

Allied to Balanoglossus are the Pterobranchia, which show a slight trace of a notochord, but no dorsal tubular nerve-cord. One of them, Cephalodiscus, has the three sets of cœlomic pouches, each with a cœlomostome, and a pair of gill-slits. It is not free-swimming but sessile, reproducing actively by budding. The other, Rhabdopleura is not only sessile but colonial, for the buds formed remain in connexion with the parent stock. Rhabdopleura has the three sets of cœlomic pouches, and cœlomostomes, but no gill-slits.

The next form to consider is Phoronis, which is worm-like with the anterior end modified into a row of tentacles. The anterior region of the body corresponding to the proboscis is reduced to a flap overhanging the mouth, so that the body contains only two sets of cœlomic pouches. The larval form of Phoronis which is called the Actinotrocha, has ciliated bands reminiscent of those of the Tornaria. Phoronis has nephridia, and as these structures are also present in Amphioxus, it is possible that they were present in the original common ancestor from which all these forms were descended.

Phoronis is related to the Ectoproctous Polyzoa, and to the Brachiopoda. All these forms, so far as is known, tend to have cœlomic pouches developed as enterocœls, and usually showing a tripartite arrangement. Many of them have open cœlomostomes. The larval forms usually have a ciliated band passing behind the mouth, and cleavage of the egg is indeterminate. These features distinguish the chordates and

Fig. 175.—A few examples illustrating the radiation of the lower chordates as aquatic animals. (Not drawn to scale.) *a*, Balanoglossus; *b*, larva of an Echinoderm for comparison with *c*, Tornaria larva of Balanoglossus; *d*, Ascidian (sessile degenerate type); *e*, restoration of Cephalaspis (Ostracoderm); *f*, typical Teleost with homocercal tail; *g*, eel; *h*, Edriolychnus (deep-sea type, with dwarf male attached to female); *i*, Raia (Selachian bottom-living type); *j*, sole (Teleost bottom-living type: "flat-fish"); *k*, Exocœtus (so-called "flying fish"). (*e* after Goodrich, *h* after Regan, simplified.)

their allies from the other great group of invertebrates comprising the Annelida, Arthropoda, and Mollusca.

There is reason to believe that the concentration of nerve-cells to form a central nervous system out of the more primitive diffuse nerve-net took place in the region of greatest stimulation. This is the ventral side in Annelida, Arthropoda, and Mollusca, all of which typically crawl on the ventral surface. The fact that the central nervous system of chordates is dorsal seems to show that the ancestral chordates were not ventral crawlers, but pursued a free-living pelagic existence, receiving the greatest stimulation on the dorsal side from the surface of the sea.

Returning now from these more or less distant allies to true chordates, the next group to consider is one which, like the Hemichordates, has left the main line of chordate evolution and become specialised in different directions: the Urochordata. These preserve the notochord in the tail in the larval stage only, and the dorsal tubular nerve-cord of the larva degenerates in the adult. They possess gill-slits, and a typical well-developed endostyle, used in connexion with the ciliary method of feeding. Their development is also typical of chordates. One group of these animals, the Larvacea, retain the larval structure throughout life, with the tail and notochord. The others pass through a free-swimming larval stage, and then undergo a retrograde metamorphosis into sessile animals, losing the tail, notochord, and larval eyes and organs of balance. These are the Ascidiacea or sea-squirts. Some of these are solitary, but most are colonial, reproducing extensively by asexual reproduction or budding, as is commonly the case with sessile forms. Others, forming the group of Thaliacea or salps, have returned to a free-swimming existence, but retaining many traces of former sessile habits ; in particular the habit of budding, which is very prevalent. Some of them have a true alternation of sexually produced (from fertilised eggs) and asexually produced (from buds) generations, and one form is further interesting in that the sexually produced generation is nourished during its development by the mother by means of a placenta (Salpa).

None of these forms, however, exhibit the typical chordate segmentation of the body, which enables them to swim in definite directions instead of being carried aimlessly about at the mercy of currents. The immediate ancestors of Amphioxus and of the higher chordates were elongated, compressed from side to side and deep from dorsal to ventral edge. As a consequence, they were able to bend the body from side to side, and perform undulatory movements. The body was made up of several segments. Each segment was separated from the ones in front and behind by septa or partitions, and stretching from septum to septum were the myotomic muscle-fibres. When the myotome on one side of a segment contracts, the septa bounding that segment come closer together, and the body becomes concave on that side. The advantage of having several segments made it possible for the body to bend in several places. By bending alternately right and left in successive regions of the body, and making the bends pass down the length of the body by throwing the myotomes into contraction in succession, the undulatory movements are produced which enable the organism to swim. These movements were made still more efficacious by lengthening the body, which was accomplished by the development of an extension behind the anus forming the tail. After bending in any place, the body became straight (before bending in the opposite direction), and this was effected not only by the relaxation of the myotome on that side, and the contraction of the myotome on the opposite side, but by the possession of a stiff yet elastic rod running along the whole length of the animal: the notochord. This is the typical primitive method of chordate locomotion which persists not only in the fish, but also in the lowest land-vertebrates.

The fact that the animal moved in a definite direction had the consequence that the front end was further specialised by a concentration of sense-organs, which ultimately was to bring about the formation of a head.

It has been held, with some degree of probability, that the habit of swimming in a definite direction was evolved in response to the constant direction of flow of water in rivers or

large estuaries, and that the evolution of the early true chordates took place in such surroundings.

The ciliary method of feeding which these animals possessed limited the size of the particles of food which they could ingest, and the size to which they could grow.

The earliest chordates of which fossil remains are known are the Ostracoderms (from the upper Silurian and Devonian), which recent work has shown to be related to the Cyclostomes, especially as regards the brain, auditory organs, and blood-vessels. This raises some interesting problems, because the Ostracoderms possessed denticles, bone, and paired fins, all of which structures are lacking in Cyclostomes. The mode of life of Petromyzon, Bdellostoma, and Myxine is undoubtedly degenerate with their sucking mouth, but they would be more degenerate than otherwise expected if they had lost the structures possessed by the Ostracoderms. The curious fossil Palæospondylus (from the Devonian) may be related to these forms, in all of which evolution had proceeded far enough for the formation of a definite head.

The first true fish appear to have been cartilaginous (together, the cartilaginous fish are called Chondrichthyes) and related to the Selachii. Among them may be mentioned Acanthodes (upper Silurian), Cladoselache (Devonian) interesting for the structure of its paired fins, and Pleuracanthus (Permian). All these forms had true biting jaws, two pairs of paired fins, and heterocercal tails. True Selachii related to Heterodontus (the Port Jackson Shark) appeared in the Carboniferous. At the present day, the Selachii are represented by the true sharks (and dogfish), and by the rays (Raia, Torpedo), which have become adapted to living on the sea bottom and have become flattened in consequence. Their pectoral fins have expanded and fused with the sides of the body. The gill-slits are on the under surface, the spiracle is above. One member of the rays, Pristis the saw-fish, has returned to an active mode of life. The angel-fish Rhina is intermediate in form between the sharks and the rays.

Another group of cartilaginous fishes diverged in the

Devonian and gave rise to the Holocephali, represented at the present day by Chimæra.

The bony fish or Osteichthyes appear in the Devonian, and the lungs which they possess were probably in connexion with the poor oxygen-content of the fresh water in which they lived. The Dipnoi were represented by Dipterus (Devonian), and the non-Dipnoan bony fish, or Teleostomi were represented by Osteolepis (also Devonian). These two forms were closely related, and they had the following characters in common : blunt lobate fins, a pair of external and a pair of internal nostrils, the general arrangement of the bones of the roof of the skull, heterocercal tails, and, most important of all, cosmoid scales. There is no doubt that they had a common ancestor, perhaps in the Silurian, and from a close relative of this ancestor the Tetrapods arose. One of the Osteolepidoti, Sauripterus, had fins from which the structure of the penta-dactyl limb of the Tetrapod might be derived. In the Cœla-canths, which are Teleostomes related to the Osteolepidoti, there is definite evidence of the presence of a lung, for it was calcified and fossilised. The Dipnoi evolved into the forms living at the present day, and became more and more adapted to life in rivers which are liable to dry up. The wide and dis-continuous distribution of Ceratodus (Australia), Lepidosiren (South America) and Protopterus (Africa) to-day is evidence of the antiquity of the group. The evolution of these forms went on parallel to that of the early Tetrapods, and inde-pendently from them.

On the Teleostome side, another group arose in the Devonian from some relatives of the Osteolepidoti : the Palæoniscoidea. These fish are characterised by the possession of scales of the type called palæoniscoid. Cheirolepis resembled Osteolepis in the structure of its skull, but its eyes were larger and the heterocercal tail was more accentuated. This pro-vision for more active swimming was probably connected with the improvement of the eyes as sense-organs. Polypterus, alive to-day, may be regarded as a descendant of the Palæo-niscoids. It has palæoniscoid scales, and preserves the open spiracle. It inhabits certain rivers in Africa. On the other

hand, the Palæoniscoids also gave rise to the sturgeons. Chondrosteus (Jurassic) is already like the sturgeon Acipenser. These animals preserve the open spiracle, but the palæoniscoid structure of the scales is lost. Sturgeons are both fluviatile and marine.

Another line of evolution from the Palæoniscoids leads to the higher bony fish or Holostei. These fish lose the open spiracle and their tails assume the homocercal pattern. At the same time the radials of the paired fins become reduced, and the web of the fin is supported mostly by the dermal fin-rays or lepidotrichia. In the median dorsal and ventral fins the lepidotrichia correspond in pairs to the radials, so that the fins can be lowered and raised. Of the Holostei, two groups are primitive. One of these contains Amia, an inhabitant of the rivers of North America. Its lung is still highly vascular and supplied by pulmonary arteries, and in the region of the tail its vertebral column consists of separate hypo- and pleurocentra. The other group contains Lepidosteus, likewise an inhabitant of North American rivers. Its scales are of the peculiar pattern known as lepidosteoid, with a covering of ganoin. The lung is vascular, but supplied by arteries from the dorsal aorta. It is worth noticing that the primitive Osteichthyes are almost exclusively inhabitants of fresh water.

In the remaining highest bony fish or Teleostei (a term not to be confused with Teleostomi), the scales lose the layer of ganoin and become thin and transparent. The lung becomes modified into a swim-bladder, and loses the vascular spongy walls characteristic of a lung. It functions as a hydrostatic organ of adaptation to different depths, and this illustrates the fact that the Teleostei are a group which has reinvaded the sea from fresh water. Rivers do not possess sufficient depth to necessitate a swim-bladder. A number of Teleosts, however, are inhabitants of fresh water, to which they have presumably returned from the sea. The Teleosts have radiated into a great many different lines, and are the most successful of the fish. They have become specialised to various modes of life, but they must be regarded as a sterile side branch on

the tree of vertebrate evolution, for their specialisations have prevented them from evolving into anything further. Although some of them, such as Periophthalmus, are capable of coming out on dry land and hobbling about, they cannot compete with the true land-vertebrates, which are less specialised but more progressive descendants of their ancestors, the pre-Osteolepids. Of the adaptations which Teleostei have undergone, one of the most interesting is the modification in connexion with the habit of living on the sea-bottom, and which has resulted in the " flat fish." When hatched, these fish, of which Solea (the sole) is an example, are normal and symmetrical in form, but they undergo a metamorphosis as a result of which they lie on one side on the bottom. The head becomes twisted so that the eye of the " underside " (right or left, according to the species) moves on to the " upper side." It is interesting to compare this flattened condition of the body with that of the rays. The modifications in the two groups are totally different, but both are adaptations to one and the same mode of life, and this accounts for what similarity there is between them.

The so-called flying fishes, of which Exocœtus is an example, have enlarged pectoral fins, and are capable of prolonged leaps through the air rather than of true flight. Lastly, attention may be called to certain deep-sea fish (Edriolychnus) which are not only of a peculiar shape, but are remarkable in that the males are dwarfed and degenerate, and live attached to the females on which they are parasitic.

LITERATURE

DELAGE, Y., et HEROUARD, E. Zoologie Concrète, 8, les Procordés. Schleicher Frères, Paris, 1898.

REGAN, C. T. Dwarfed Males parasitic on the Females in Oceanic Angler-Fishes. Proceedings of the Royal Society, B, vol. 97, 1925.

CHAPTER XXXVIII

THAT the amphibia arose from fish there is no doubt, and their ancestor must have been one of the primitive Osteichthyes, related to the stock which also gave rise to Osteolepis and Dipterus. For purposes of comparison Osteolepis may be taken as approaching the structure of this ancestor.

The resemblances between Osteolepis, on the one hand, and one of the earliest Stegocephalian amphibia such as Loxomma on the other extend to the following features. In both, the skull is a complete bony box, the dermal bones of which can in most cases be identified with certainty because the amphibia also had lateral-line canals which occupied grooves in the bones. The bones of the palate are similar, and both had nostrils which lead through into the cavity of the mouth. The amphibian Eogyrinus had a shoulder girdle the dermal bones of which were attached to the post-temporal bone of the skull by the supra-cleithrum, as in the fish. Also, these early amphibia had no sacrum, for the ilium was not attached to the ribs. The walls of the teeth were folded, in the Labyrinthodont pattern. The amphibia are autostylic, as are the Dipnoi including Dipterus. The otic process in Osteolepis did not reach the auditory capsule, however, and it is a question as to whether the common ancestor of Osteolepids, Dipnoi, and Tetrapods was autostylic or not. A lung was almost certainly present in Osteolepis.

The ancestor of the Tetrapods must, however, have had pectoral and pelvic fins equally developed and similar in structure, and this condition has not yet been found in any Osteolepid (or other) fish. The really distinctive feature of

all the Tetrapods is the possession of limbs ending in five digits, and it has already (see p. 315) been shown that the skeleton of the pectoral fin of the Osteolepid fish Sauripterus is such as to render it easy to suppose that the pentadactyl limb arose from a fin like that of the Osteolepids. Osteolepis is Devonian, and the earliest known amphibia are from the Lower Carboniferous. It is fairly certain, therefore, that at some time in the Devonian, fish living in the estuaries and fresh-water basins became subjected to the desiccation which characterised this period. They were able to breathe atmospheric oxygen
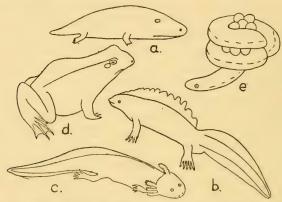
FIG. 176.—A few examples of different types of Amphibia. (Not drawn to scale.)

a, restoration of Stegocephalian ; b, male newt in breeding season (Urodele) ; c, Amblystoma (larval form or Axolotl showing the external gills) ; d, frog (Anuran) ; e, Ichthyophis (Gymnophiona). (e after Sarasin).

by means of their nostrils and lungs, and as they floundered about in the mud, the number of rows of radials in their fins became reduced to five, separate from one another instead of being united by the web of a fin. The persistence of the lateral-line canals shows that these animals still spent much of their time in the water, and their excursions on land probably took the form of wandering from pond to pond. In fact, the amphibia never succeeded in making themselves completely independent of water, and for three reasons. In the first place the eggs had to be laid in water, and the larval

stages which breathed by gills required then, as they do now, a watery medium. Next, fertilisation was external, and for the sperms to be able to find the eggs, there must be a liquid medium for them to swim in. Lastly, amphibia breathe largely through their skins, and these must be moist to enable the gaseous exchange to take place.

The transition from water to air necessitated a development of the olfactory organs to greater sensitiveness, for the concentration of substances in water is very much greater than that which can be obtained in air. The result was an increase in development of the olfactory organs and of the corresponding centres in the forebrain. The latter development accompanied and perhaps assisted the formation of the cerebral hemispheres, which are regarded as connected with an adaptation to the poor oxygen-content of the water in which the amphibia and their ancestors evolved.

It appears, therefore, that the transition from aquatic to terrestrial life was accomplished without any very striking changes or modification of organs, but it must be remembered that the function of these organs is controlled by the pattern of nerve-fibres in the central nervous system, and it becomes necessary to inquire whether the transition necessitated any great neurological rearrangement. Two aspects of the transition will be considered, regarding breathing and locomotion. In connexion with respiration, it will be remembered that the amphibia breathe by means of respiratory movements performed by the visceral muscles in the floor of the mouth, in a manner very similar to that of the fish. The only real difference is that whereas the fish take in water and pass it back and out through the gill-slits, the amphibia take in air and pass it back and into the lungs. The mechanism is the same, and it is obvious that the transition from water to air involved no functional rearrangement of importance as regards respiration.

The same holds true with regard to locomotion. The amphibia were clumsy sluggish beasts with bodies disproportionately large in comparison with their limbs. As a consequence, the body was not supported by the limbs but its ventral surface dragged along the ground. The limbs stuck out at

2 F

right angles to the body, and as the body performed the same undulatory movements by means of the myotomes as does a fish when swimming, the limbs were moved forwards and backwards. In other words, the limbs were used as oars to row the animal along on land, and the same muscles and nervous connexions came into play as in the aquatic ancestor. In the very earliest Amphibia, the sacrum was absent (*e.g.* Eogyrinus). In the others it was present, and by anchoring the pelvic girdle on to the vertebral column, it strengthened the hind limbs.

One consequence must be mentioned of the possession of an autostylic method of suspension of the jaws, and of the abolition of branchial respiration and the closure of the visceral clefts, in particular the spiracle. The hyomandibula being no longer required to suspend the quadrate from the auditory capsule, its function became converted into that of conveying vibrations from the skin covering the spiracular cleft to the auditory capsule. In this way the hyomandibula became the columella auris ; the covering of the spiracular cleft became the tympanic membrane, and the cavity of the spiracular cleft became the middle-ear and Eustachian tube ; all quite simply and without involving any great rearrangement. So the ear became an organ for the delicate appreciation of sound as well as balance.

The early amphibia had a covering of dermal bones more or less all over the body. The vertebral column of the earliest forms or Embolomeri is remarkable in that each vertebra possessed two centra. There was an anterior hypocentrum and a posterior pleurocentrum. The later amphibia preserved the hypocentrum at the expense of the pleurocentrum, which disappeared. It will be seen that in the reptiles the opposite occurred.

Collectively, the early amphibia are known as the Stegocephalia or Labyrinthodonts, the former term referring to the complete bony covering of the skull. They flourished in the Carboniferous, and persisted until the Triassic period, when they were extinguished by the competition of their more successful descendants the reptiles, leaving only the frogs

(Anura), newts (Urodela) and Gymnophiona alive to-day. An important feature in the amphibia is the outgrowth from the gut to form a bladder. It is homologous with the allantois of the Amniotes.

With regard to the living amphibia, it is most important to realise that they have departed far from the primitive type of their Stegocephalian ancestors. This is shown by the great reduction in the bones of the skull and other parts of the skeleton. The Gymnophiona have evolved a worm-like burrowing habit ; the frogs have become modified in connexion with the habit of leaping with the hind legs, and the newts have become secondarily readapted to living in water, even going so far as to develop median fins which differ entirely from those of fish in not possessing radials or dermal fin-rays. Now, in several points, the newts of to-day resemble living Dipnoi (such as Ceratodus) very closely. It is of the utmost importance, however, to realise that these resemblances are due to parallel evolution and convergence, and not to genetic affinity. It is only necessary to look at the list of specialised characters of Ceratodus to see that forms like it could not have given rise to the Tetrapods : they are cousins and not ancestors. Similarly, an examination of the specialised characters of Triton and a comparison between it and the Stegocephalia show that all the points in which Triton resembles Ceratodus have been evolved within the amphibia, and a long time after the amphibia came on land.

LITERATURE

WATSON, D. M. S.   The Structure, Evolution and Origin of the Amphibia. Philosophical Transactions of the Royal Society, Ser. B, vol. 209, 1919.
——   The Evolution and Origin of the Amphibia. Philosophical Transactions of the Royal Society, Ser. B, vol. 214, 1926.

CHAPTER XXXIX

THE EVOLUTION OF THE REPTILES

THAT the Reptiles were evolved from the amphibia there is no doubt whatever, and indeed, in some cases it is difficult to decide whether a fossil is an amphibian or a reptile. The most important distinctive features are the fact that the centra of the vertebral column are formed from the pleurocentral elements while the hypocentral elements are very much reduced, and the absence of grooves for lateral-line canals on the skull. This latter point shows that the reptiles had become definitely terrestrial. They emancipated themselves from the water by overcoming the three obstacles which checked the amphibia ; viz. the necessity of water for breathing, for copulating, and for the embryo to develop in.

The first of these was countered by a better development of the lungs and the adoption of the method of expanding the thoracic cavity by means of the ribs, for replenishing their content of air. The skin was thus enabled to become dry and horny, and to be of greater efficiency in protection.

The next difficulty was surmounted by the development of copulatory organs with which the sperm could be inserted straight into the oviducts of the female, and fertilisation was internal. The sperm swam to the egg in the mucous fluid of the oviduct instead of in the pond water.
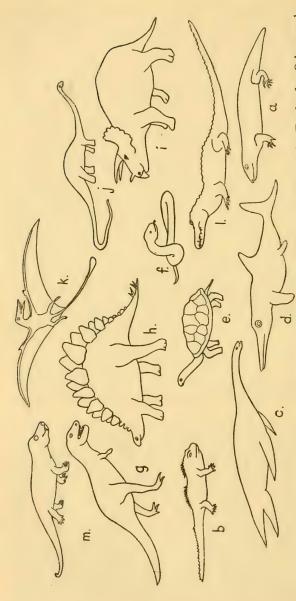
The last obstacle was overcome by a group of adaptations. The egg was laid on land, and the albumen surrounding it was itself surrounded by a shell composed of lime salts secreted by the oviducts. In this way the egg was protected from drying up, and from becoming flattened and collapsed like a " poached egg," which it would otherwise be. The embryo became

surrounded by upgrowths of the blastoderm forming the amnion and enclosing the amniotic cavity. The embryo developed in the fluid contents of this cavity, which may thus be regarded as an artificial enclosed pond. The food requirements of the developing embryo were met as in lower forms by a store of yolk in the yolk-sac. This entailed no new modifications by itself, but as embryonic development took a longer time, the quantity of yolk in the egg was relatively greater and this necessitated the modification of the process of gastrulation, and the formation of a primitive streak. There remained the difficulty of breathing, for although the gill-slits were developed they opened into the amniotic cavity, the oxygen-content of which could not be renewed. The problem was solved by the development of the allantois, representing the bladder of the amphibia. The allantois became applied to the inner surface of the porous shell, and as it was highly vascularised, the respiratory exchange took place in it. At the same time, the allantois served as a receptacle for the non-volatile excretory products of the embryo during development. Because of these structural adaptations, the reptile does not pass through a metamorphosis, but hatches from the egg as a more or less perfect miniature replica of the adult.

In the reptiles, the head is capable of extensive independent movement, and a definite neck is formed. In this connexion, the two first vertebræ become modified into the atlas and the axis.

The most primitive known reptile is Seymouria (Permian), and it is remarkable for the fact that its characteristics are not intermediate between those of amphibia and of reptiles, but some of its characters are frankly amphibian and others reptilian. Seymouria is therefore a mosaic transitional form. It is probable that the transition from amphibia to reptiles took place in the Carboniferous.

Seymouria belongs to the group of Reptiles known as the Cotylosaurs, and they preserve the complete covering of dermal bones over the skull which they inherited from their Stegocephalian amphibian ancestors. The nature of the skull is of importance in tracing out the lines of evolution of the

Fig. 177.—A few examples illustrating the radiation of the reptiles. (Not drawn to scale.) (Partly after Osborn and Lull, simplified.)

a, restoration of Seymouria (cotylosaur); b, Sphenodon; c, restoration of Plesiosaur (aquatic adaptation); d, restoration of Ichthyosaur (aquatic adaptation); e, tortoise (Chelonian); f, snake (Ophidian); g, restoration of Tyrannosaurus (Dinosaur); h, restoration of Stegosaurus (Dinosaur); i, restoration of Triceratops (Dinosaur); j, restoration of Diplodocus (Dinosaur); k, restoration of Pterosaur (aerial adaptation); l, crocodile; m, restoration of Cynognathus (Theromorph).

reptiles, and those forms in which the roof is complete and imperforate are often grouped together as the Anapsida.

The Chelonia are often classified among the Anapsida because their skull-roof is not fenestrated, although it may be reduced by emargination ; *i.e.* bones may be lost round the edge but there is no separation of bones by a perforation forming a fossa.   The Permian fossil Eunotosaurus which had osteoscutes and expanded ribs appears to be intermediate between Cotylosauria and Chelonia.   The Chelonia preserve the osteoscutes (which covered the body of the Stegocephalia) and they contribute to the formation of the carapace which is so distinctive a feature of the Chelonia.   The Triassic Triasso-chelys still had teeth and the cleithrum ; these structures are absent from existing forms.   The clavicular pectoral girdle of existing Chelonia, consisting of clavicles and interclavicle, is associated with the ventral covering of osteoscutes that form the plastron.   The scapular pectoral girdle consists of a cora-coid and a scapula bearing a large process as big as itself, directed forwards and inwards.   This girdle and the pelvic girdle are remarkable in that they are situated within the ribs instead of outside them as in normal forms.   It is interesting to note that some Chelonia have become secondarily adapted to life in water, and their limbs have been modified into paddles or flippers, as in the turtles.

The osteoscutes of the carapace are covered by corneo-scutes (" tortoise-shell ") except in Sphargis, the " leathery turtle," which form is further interesting in that the carapace attached to the expanded ribs as in other Chelonia is not present. Instead there is a bony shell formed of a great many little poly-gonal osteoscutes bearing no relation to the ribs.

The 5th metatarsal is hook-shaped in the Chelonia, but normal in the other Anapsida (Cotylosauria).

The next group of reptiles to consider is the Synapsida. They are characterised by the fact that the skull-roof is per-forated by one inferior temporal vacuity or fossa, on each side, and the 5th metatarsal is normal.   Here belong the Plesiosaurs and Theromorphs.

The Theromorphs are a very important group.   They

appear in the Permian, and preserve many primitive characters. They may have a precoracoid as well as a coracoid in the shoulder girdle, and some even retain the cleithrum. The most highly developed forms are the Theriodonts, which are the ancestors of the mammals, and they foreshadow the characters of the latter in many respects. The skull had two occipital condyles, a false palate was present, and the teeth were modified into incisors, canines, premolars and molars. The dentary was large and beginning to take on the articulation with the squamosal, while the quadrate became small and loose. In the pelvic girdle the ilium showed the mammalian character of pointing forwards, and the limbs were long and supported the body clean off the ground. A typical Theriodont is Cynognathus, but it is probable that several of its characters were evolved parallel with the mammals, having been derived from a more primitive ancestor common to it and to the mammals.

Among Synaptosauria, the Sauropterygia or Plesiosaurs have become secondarily adapted to an aquatic mode of life. They preserve primitive features such as the gastralia, which are remnants of the ventral dermal bones or osteoscutes of the Stegocephalian amphibia, but their limbs become modified into paddles. This modification has not proceeded as far in the Triassic Nothosaurus as in the Jurassic Plesiosaurus. The Plesiosaurs reached lengths of 50 feet.

In the next group or Parapsida, the roof of the skull was perforated by a single superior temporal vacuity, above the postorbital and squamosal bones. The hind border of the vacuity is formed by a bone concerning the homology of which doubt remains (see p. 104), but which may be the supratemporal. Here belong the Ichthyosaurs and the Squamata (Lacertilia and Ophidia).

The Ichthyosaurs are primitive in retaining the gastralia, and a foramen for the pineal eye between the parietals, but otherwise they are specialised in adaptation to an aquatic mode of life. Median dorsal and tail-fins are developed, and the limbs become modified into paddles, so much so that it is impossible to determine the nature of the 5th metatarsal. A series of progressive modification can be traced from the

Triassic Mixosaurus, through the Jurassic Ichthyosaurus to the Cretaceous Ophthalmosaurus. They reached lengths of 30 feet.

All the Squamata which possess limbs have a hook-shaped 5th metatarsal. The first group of these are the Lacertilia, first appearing in the Jurassic, and represented now by the lizards, geckos, and chamæleons. In the Cretaceous, a group of Lacertilia became adapted to an aquatic life,—the Mosasauria. They reached a length of as much as 40 feet, and their limbs became modified into paddles. The second group of the Squamata are the Ophidia or snakes. It is characteristic of the Squamata that the quadrate is loose, and in the Ophidia the two halves of the lower jaw are separate, which enables relatively enormous mouthfuls to be swallowed.

The remaining reptiles form the group Diapsida, for their skull roof is perforated by two temporal fossæ or vacuities on each side. So far as is known, all of them have a hook-shaped 5th metatarsal. Here belong the Rhynchocephalia, the Crocodilia, the Dinosaurs and the Pterosaurs, and the Diapsida also contained the ancestors of the birds.

The Rhynchocephalia appear in the Triassic with Rhynchosaurus, and are represented to-day by Sphenodon. They are primitive in retaining the gastralia. The Triassic Thalattosaurs, which had paddle-like limbs, were probably related to the Rhynchocephalia.

The Crocodilia form a large group of generalised reptiles, possibly dating back to the Permian. The Triassic Pseudosuchia, of which Euparkeria is an example, are regarded as related to the ancestors of the Rhynchocephalia, the Dinosaurs and Pterosaurs, the existing crocodiles, and the birds. The living crocodiles and alligators retain the gastralia, and other dermal ossifications. Mention may be made of the Jurassic Thalattosuchia, yet another group of reptiles which became secondarily adapted to aquatic life with paddle-like limbs.

The Dinosaurs were the dominant animals in the Jurassic and Cretaceous. The skull had two temporal vacuities on each side, and in addition a prelachrymal vacuity. Some were quadrupedal and herbivorous, such as Diplodocus

(Jurassic), reaching the immense length of 90 feet. Others were carnivorous with formidable teeth, and the hind limbs larger than the fore limbs, so that they were probably bipedal. An example of such a form is Tyrannosaurus, Cretaceous, reaching almost 50 feet in length. The foregoing types of Dinosaurs had a pelvis of normal shape, and are grouped together under the term " Saurischia." The remainder, Predentata (or Ornithischia), have an additional postpubis which stretches back beneath the ischium, and a predentary bone in the lower jaw. The Predentata include the herbivorous bipedal Iguanodon from the Cretaceous, over 30 feet long ; the absurd-looking Stegosaurus with its armour of large bony plates (Jurassic, 20 feet long) ; and the horned Triceratops (Cretaceous, 25 feet long).

The Pterosaurs were closely allied to the Dinosaurs, and like them had a pair of temporal vacuities and a prelachrymal vacuity on each side. They also preserved gastralia, and while some had teeth others were toothless. The fore limbs were modified for flying, by means of a web of skin stretched from the greatly elongated fourth finger. The Cretaceous Pteranodon had an expanse of wings measuring 25 feet. Of all this enormous wealth of reptilian life which dominated the land, water, and air, in the Jurassic and Cretaceous periods, only the Squamata, the Chelonia, the Crocodilia, and the Rhynchocephalia have survived, and in very reduced numbers. The rest went extinct before the Eocene. It may be that a reduction of temperature put an end to them, or that the food supply became deficient. Certain it is that their brains were ridiculously small, and they can have been no match for the small and agile mammals in intelligence.

Two main points for consideration arise out of a study of the reptiles. The first concerns the structure of the 5th metatarsal bone. In the Cotylosaurs it was of a normal shape, as also in the Synapsida. Now, the Synapsida are to be regarded as having been derived from the Cotylosaurs, and one group of them, the Theromorphs, gave rise to the mammals. The line of mammalian descent is therefore characterised by the possession of a normal-shaped straight 5th metatarsal.

On the other hand, the other reptiles such as the Chelonia, together with the Squamata, and all the Diapsida have a hook-shaped 5th metatarsal. The birds were derived from a Diapsid stock, and so it may be said, therefore, that the line of avine descent is characterised by the possession of a hook-shaped 5th metatarsal. Actually what this modification means or what function it serves is unknown, but it is to be noticed that among the animals possessing it are forms which live on land, in the water, and in the air, so that it would seem not to have an adaptive significance, nor to be capable of modification by different modes of life. It looks, therefore, as if it could be used as a diagnostic feature inherited from a common ancestor by all the forms possessing it. This common ancestor was probably a late Anapsidan, and the importance of this matter is that from this point onwards the reptiles were divided into two main and divergent branches. One branch which may be called the Sauropsidan includes the Chelonia, the Parapsida, the Diapsida, and the birds. The other or Theropsidan branch includes the Synapsida perhaps (the Synaptosauria), and the mammals. As a result of these considerations, it appears that the term " Reptilia " is applied not so much to a unified group of related animals as to two divergent stocks. It therefore refers to a grade of structure and degree of evolution ; and when the knowledge of fossil forms is more complete, it will be possible to abolish the class " Reptilia," or to restrict it to the primitive Anapsida, and to substitute the classes " Sauropsida " and " Theropsida," containing the birds and mammals respectively.

That these conclusions are sound is shown by a consideration of the aortic arches. It is to be noticed that all the living reptiles belong to the Sauropsidan branch, and in all of them the systemic aorta is split into two right down to the ventricle of the heart. The result is that there are right and left systemic arches springing respectively from the left and right sides of the ventricle. The condition of the bird fits into this scheme, for it differs from the arrangement in the crocodile only by the loss of the left arch. Now, in the mammal, the systemic aorta is single and undivided. The point is that it is impossible to

derive the Sauropsidan type of aorta from the mammalian, or vice versa, and it is necessary to go back to a primitive type like that of the amphibia where the aorta is not only undivided but the pulmonary arch has not yet become separated off. The primitive Cotylosaurs may have been of this type. It is certain that the Synapsida must have resembled the mammal (for the latter was derived from the former), and therefore differed from the Sauropsida as regards the structure of the aortic arches. This is the same divergence which appeared from a consideration of the hook-shaped 5th metatarsal.

LITERATURE

GOODRICH, E. S. On the Classification of the Reptilia. Proceedings of the Royal Society, Ser. B, vol. 89, 1916.

NOPCSA, F. Die Familien der Reptilien. Fortschritte der Geologie und Palæontologie, 2, 1923.

WATSON, D. M. S. On Seymouria, the Most Primitive known Reptile. Proceedings of the Zoological Society, London, 1918.

CHAPTER XL

THE EVOLUTION OF THE BIRDS

THE birds present so many similarities to the reptiles that they have been classified together with them in the group Sauropsida. The resemblances extend to the following features. The heart and arteries of the bird are the same as those of the crocodile with the exception of the left systemic arch, which in birds is abolished. The perivisceral cœlomic cavity of birds is divided up into pulmo-hepatic recesses and pleural cavities, by means of the pulmo-hepatic ligaments and oblique septa ; this arrangement is also present in the crocodile. The lung of birds gives rise to a number of diverticula or air-sacs which ramify about inside the body ; small air-sacs are formed by the lung of the chamæleon. With regard to the nervous system, the brain of birds is an elaboration of the grade of structure shown by the brain of crocodiles, and its distinctive feature is that the corpus striatum has been especially developed while the cerebral cortex remains small and thin. The cerebellum of birds presents many resemblances to that of the Pterosaurs, which can be explained as due to the action of similar modes of life working on related materials. The early stages of development, amnion and allantois, are very similar. Coming to the skeleton, the single occipital condyle, the inter-orbital septum, the limb girdles, the hollow nature of several of the bones and the mesotarsal articulation of the feet, are all characters which appear in some or most of the reptiles of the Sauropsidan branch. In addition, the Jurassic fossil Archæopteryx had gastralia, a prelachrymal and remnants of two temporal vacuities, a long tail with several separate caudal

445

vertebræ, and a lower jaw perforated by a foramen as in croco-diles. It is possible that Archæopteryx had cartilaginous uncinate processes on its ribs.

Nothing can be regarded as more certain than that the birds were evolved from reptiles of the Sauropsidan branch, and the only point left to consider in this connexion, is which.

Birds share with :—

Crocodiles : the structure of the heart and arteries, the arrangement of the cœlom, the large corpus striatum, the foramen in the mandible (of Archæopteryx) ; and according to the precipitation blood-tests a high degree of blood-relationship ;

Dinosaurs : the prelachrymal fossa, the mesotarsal articulation, the hollow bones, and the bipedal mode of progression ;

Pterosaurs : the structure of the cerebellum ;

Rhynchocephalia : the uncinate processes of the ribs ; with all the above-mentioned reptiles, the two temporal vacuities.

Now, the ancestors of all these reptiles were probably closely allied to the Pseudosuchia, of which Euparkeria is an example from the Triassic ; and it is very probable that these forms were the ancestors of the birds also.

The characteristic of birds is their peculiar method of flight, and most if not all of their modifications are adaptations to life in the air, foremost among which are the feathers.

Feathers are one of the most marvellous cases of adaptation known in the animal kingdom. Firmly anchored by the rachis or quill to the skeleton of the forelimb, the vane of the feather gives perfect air-resistance at the downstroke coupled with lack of resistance in the upstroke. The feather is proverbially light, and the structure of the hooks or hamuli and barbules enables the feather to be repaired if damaged, by the bird itself, by simply drawing the vane through the beak. The result of this process is to rehook the hamuli on to the barbules should the barbs have become torn apart.

Other feathers are smaller and serve not for flight but as a non-conducting layer for heat, and enable the bird to maintain

a constant and high internal temperature. Birds are homo-thermous. This condition with its consequent increased efficiency of muscular and nervous processes is necessitated by the great exertion required to maintain the weight of the body in the air during flight.

This was accomplished with the aid of the feathers by the perfection of the vascular system (abolition of the left systemic arch) and the development of the air-sacs. The latter ensure a complete " blow-through " of the lungs and avoid the inefficiency due to the presence of stagnant residual air in blind-ended sac-shaped lungs. Further, the air-sacs assist in regulation of the internal temperature by varying the amount of heat lost.

The characteristic development of the keel (carina) on the sternum in flying birds is a direct adaptation to the need for a firm origin for the large muscles concerned with flight.

As to the evolution of the method of flight itself, there is not yet any certainty, and several theories have been pro-pounded.

The avine method of flight differs from that of all other forms in that no use is made of stretched membranes. From a study of the feathers and scales on the leg of the ostrich, there is reason to believe that feathers were evolved in con-nexion with scales, but not from them. Be that as it may, the development of feathers must have resulted in an increase in the surface of the animal without any material increase in its weight. It is easy to see how this would have benefited the ancestral birds if they inhabited trees and were in the habit of leaping or parachuting from one branch to another. At the same time it must be remembered that the structure of the pelvic girdle and limbs of the bird are adapted to a cursorial mode of life with a bipedal method of walking or running. The biological success of birds is probably due in no small measure to the fact that the adaptations for flight in no way interfere with or involve the hind pair of limbs. The ancestors of the birds must therefore have been terrestrial and cursorial in habits before becoming arboreal.

The early birds like Archæopteryx (Jurassic) had a long tail, jaws garnished with teeth, wings with three well-formed fingers ending in claws, and a more or less flat sternum. At the present day, birds have no teeth, and their tails are shortened up, the fused vertebræ forming the pygostyle.

Living birds are divided into two groups : Palæognathæ, and Neognathæ, according to the structure of the palate. In
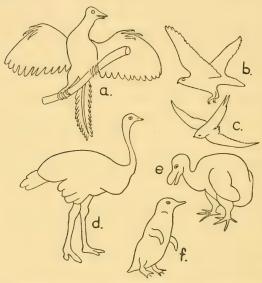
FIG. 178.—A few examples of different types of birds (not drawn to scale).

a, Archæopteryx ; *b*, bird of prey ; *c*, swift ; (both *b* and *c* are examples of the Neognathæ showing highly perfected aerial adaptation) ; *d*, ostrich (Palæognathæ, flightless) ; *e*, dodo (one of the Neognathæ which lost the power of flight) ; *f*, penguin (aquatic adaptation). (*a* after Pycraft.)

the former (which include what used to be called the " flight-less birds " or Ratites, plus the Tinamus), the prevomer is large and touches the pterygoids ; whereas in the latter (the so-called Carinates minus the Tinamus) the prevomer is small and does not touch the pterygoids. In Tinamus and Neognathæ the sternum bears a large keel or carina, on to which the pectoral muscles (which are used in flight) are attached, and the well-developed clavicles fuse together at their base to form

the " merrythought " or furcula. The carpals, metacarpals, and phalanges are much reduced and fused together, but in the young Hoatzin (South American) among others, the hand is well developed and represented by three digits ending in claws. With the help of these claws the young Hoatzin clambers about on trees in a manner suggestive of the presumed habits of its ancestors. The barbs of the flight-feathers are connected to one another by the hooks on the barbules, and most of them are active flyers. All make nests of one kind or another and incubate the eggs, except the cuckoo which is parasitic in that it lays its eggs in the nests of other birds for them to incubate, and the Megapodes which lay their eggs in decaying vegetable matter, relying on the heat engendered by the latter to incubate them.

A point of no small importance in these birds is the high development of courtship-activities and structures, which play a large part in knitting parents together into a family. Normally it is the male which is the active partner in courtship and possesses well-developed " secondary sexual " or courtship characters. In some, such as the Great Crested Grebe, males and females are similar in appearance and in the ardour of their behaviour. In others, of which the Phalarope is an example, the female is the more brilliant and active, and the male incubates the eggs, and in fact does almost everything except lay them.

As regards their anatomy, these birds are very much alike ; so much so that it is a matter of extreme difficulty to arrive at a satisfactory scheme of classification for them. This is partly because the birds are a comparatively recent group, and because they have been so successful in the walk of life to which they have become adapted that little extinction has taken place. Most of them are strictly aerial animals. Others such as the common fowl and the extinct Dodo of Mauritius have secondarily become terrestrial as a result of reduction of the powers of flight. Many have become adapted to swimming on water, and have developed webs of skin between the toes of the feet, which are then described as webbed feet. This has taken place independently in a great many groups,

such as the Petrels, Penguins, Divers, Cormorants, Flamingos, Ducks, and Gulls.

In the Penguins, in addition, the wings have been modified into paddles or flippers and the birds can no longer fly. It is worth noticing that these aquatic birds, with the exception of the penguins, have their powers of flight in no way impaired by the adaptation of webbed feet ; this is a consequence of the avine structure of the wing which leaves the hind limbs unencumbered. A peculiar modification which may occur is the absence of the 5th flight-feather carried on the ulna (5th secondary remex). This condition is known as aquinto-cubitalism or diastataxy, and it occurs sporadically in some groups and not in others, or even in some members and not in others of the same group. The significance of this modification which is so peculiar is a mystery.

The Palæognathæ include the Struthiones (Ratites) or " flightless birds " and the Tinamus. In the former the flight-feathers have lost the hamuli on the barbules, so that the vanes are no longer resistant to the air. This character is associated with the loss of the power of flight on the part of these birds, and accounts for the well-known structure of the ostrich plume. Also connected with their flightless condition, the Palæognathæ (again with the exception of the Tinamus) have lost the keel on the sternum. These characters are specialisations and losses from a more primitive type of flying bird. At the same time the palate of the Palæognathæ is more primitive than that of Neognathæ, and some preserve primitive characters such as the claws at the ends of the fingers in the wing in the ostrich. In addition to the ostrich (Struthio, South African and Arabian), the Struthiones include the Rhea (South American), the Emu and Cassowary (Australasian), and the Kiwi (Apteryx, New Zealand). The extinct Moa of New Zealand had reduced its wings altogether.

It is interesting to note that some Neognathæ also lost the power of flight, such as the extinct Dodo of Mauritius, and the Solitaire of Rodriguez. Flightless birds, whether Palæognathæ or Neognathæ, are more or less restricted to the southern hemisphere or to islands, where there is little competition to

fear from other animals. Their degeneracy was therefore, so to speak, allowed because of the greater leniency of natural selection in these regions.

LITERATURE

HEILMANN, G.   The Origin of Birds.   Witherby, London, 1926.
PYCRAFT, W. P.   A History of Birds.   Methuen, London, 1910.

CHAPTER XLI

THE EVOLUTION OF THE MAMMALIA

In considering the evolution of the mammals it is necessary to revert to the Theromorph reptiles, in the more highly developed members of which, such as Cynognathus, it was found that the following characters were present. The skull had two occipital condyles, a false palate, heterodont teeth in sockets with the mammalian method of replacement. The dentary was large, the remaining membrane-bones of the lower jaw were small, and the jaw articulation was beginning to be taken on by means of the squamosal ; the quadrate was loose and small. The limb girdles were of the mammalian type, and the limbs were long and supported the body clean off the ground. These characters point unmistakably to the fact that the mammals were derived from ancestors which were Theromorph reptiles.

The dominant factor in mammalian evolution appears to have been the development of the brain along the lines of increase in size of the roof of the cerebral hemispheres, and the formation of a special area of cerebral cortex called neopallium, which was no longer under the dominance of the fibres coming from the olfactory centres. The neopallium became an organ for the retention of past sensations and for the delicate co-ordination of the activities of the body of the animal, which thus became capable of more efficient response to external sets of circumstances, and capable of profiting by experience. It enabled the animal to improve the speed and precision of its method of locomotion with the help of the long and delicately formed limbs ; and the fact that the skin lost its hard horny scales and became supple and covered with hairs, enabled it to

increase its sensitiveness. The hair covering, furthermore, was a non-conductor of heat, and this fact together with the greater activity of the animal and more intense metabolism enabled the mammals to become warm-blooded. Later on, with the development of the sweat-glands in the skin, the mammals were able to regulate their loss of heat, and so become constant-temperatured or homothermous. The modification of some of the skin-glands into mammary glands made it possible for the young mammals to pass through a protected period of infancy during which the finishing touches to their development were put on, and they became apprenticed under the care of the family to the conditions of their adult life.

The transition from Theromorph reptiles to mammals probably took place in the Permian period, for in the Triassic, fossils are found which show an advance in grade of structure. Of these, the Multituberculata are a group which persisted until the Eocene. They advanced in general evolution and grade of structure as far as the Marsupials. The pelvis was narrow as in the reptiles, and the lower jaw which contained a single bone, had inflected angles. The single bone (dentary) in the lower jaw is a characteristic mammalian feature. The Multituberculata were, however, specialised, and possessed molar teeth with a large number of cusps. They are probably a divergent line which evolved parallel with but independently from the remaining mammals.

At this stage it must be imagined that the primitive mammals had seven cervical vertebræ as a constant number, and that they had evolved the characters enumerated above, together with the diaphragm and the non-nucleated red blood-corpuscles. The epipterygoid had been converted into the alisphenoid, and the quadrate (incus) and articular (malleus) into auditory ossicles. They retained, however, the reptilian characters of the presence of the coracoid, precoracoid, and interclavicle, the cloaca and the habit of laying eggs. They had not yet evolved the viviparous habit or the formation of a placenta, epiphyses were not yet well developed in the bones, the mammary glands were unprovided with teats, and the two
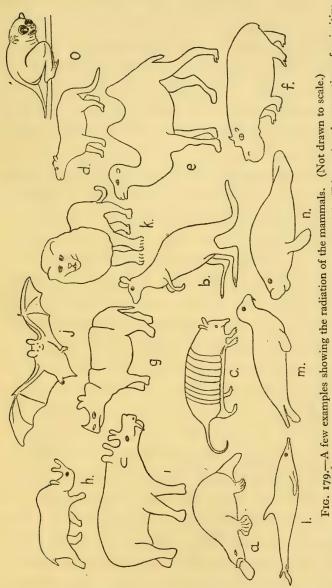
halves of the neopallium were not connected by that special transverse commissure : the corpus callosum.

The Monotremes must have diverged from the main stem at this point, and they are represented to-day by Ornitho-rhynchus and Echidna, to which the description just given fits well. They are inhabitants of the Australasian region.

The remaining mammals were the ancestors of the Marsupials and of the Placentals. These two groups are fairly closely allied, and have the following characters in common : the mammary glands have teats, they are viviparous, a placenta of some kind is present, the ear has an external pinna, the bones mostly have epiphyses ; the coracoids, interclavicle, and cloaca have been lost.

It is clear from the reduction of the milk-dentition and of the allantoic placenta (which is only preserved in Perameles) in Marsupials, that they are derived from a stock with two sets of teeth and with a well-formed allantoic placenta. On the other hand, some primitive Placentals show evidence of descent from forms with marsupioid characters, such as alleged traces of a marsupial pouch, of coracoids, and other features. The conclusion to be drawn is that Marsupials and Placentals had a common ancestor perhaps in the Jurassic. Now, in the Jurassic the fossil Trituberculata are found, and they are regarded as related to the Marsupials by some, and to the Insectivores (Placentals) by others. The number of teeth was large. The Trituberculata which derive their name from the pattern of the cusps on the molars were probably related to the common ancestors of Marsupials and Placentals. It is a significant fact that the arrangement of the cusps on the molar teeth in several primitive groups of mammals is of this type, regardless of the diet for which the teeth of the higher members of these groups are modified. Molars with separate cusps like this are called bunodont.

In the Eocene period, the Marsupials had a wide distribution over the earth, but at the present day they are restricted to the Australian and southern and central American regions. These regions are characterised by their isolation and the comparative absence of mammals of the Placental type. If it

FIG. 179.—A few examples showing the radiation of the mammals. (Not drawn to scale.)

a, Ornithorhynchus (Monotreme); *b*, kangaroo (Marsupial); *c*, armadillo (Edentate); *d*, restoration of primitive Condylarth; *e*, camel (Artiodactyl Ungulate); *f*, hippopotamus (Artiodactyl Ungulate); *g*, rhinoceros (Perissodactyl Ungulate); *h*, restoration of Titanotherium; *i*, restoration of Uintatherium (Amblypoda); *j*, bat (Cheiroptera); *k*, lion (Carnivora); *l*, dolphin (Cetacea); *m*, seal (Carnivora pinnipedia); *n*, Sirenian; *o*, Tarsius (Primate). (*d*, *h*, and *i* after Osborn; *o* after Shelford.)

had not been for the latter fact, there is little doubt that the Marsupials would have become extinct, for they cannot compete with the Placentals. Instead, in the security of their isolation, they radiated out into a number of types which are especially interesting in that they have evolved parallel with several groups of Placentals, and by becoming adapted to equivalent biological environments have developed a convergent resemblance to these Placentals. Nearly all Marsupials have a marsupial pouch in the female and epipubic bones supporting it.

The opossum (Didelphys) and Cænolestes are American ; all the remainder are restricted to Australasia, though fossils related to these are also found in South America. Dasyurus is the Marsupial equivalent of the cats, while the dogs are represented by Thylacinus, Perameles (the bandicoot) is an attempt at a rabbit, Petaurus (the phalanger) resembles the flying squirrels, while Notoryctes is a remarkable imitation of the mole. Phascolarctos (the koala) is the " marsupial bear," Phascolomys (the wombat) is the " marsupial rodent," the extinct Thylacoleo was the " marsupial lion," while Macropus (the kangaroo) represents the swift-moving Ungulates.

The Cretaceous strata of Mongolia have revealed fossils of apparently Placental mammals, of which Deltatheridium is an example, and which can be regarded as intermediate between the Jurassic Trituberculata and the true Placentals of the Eocene.

The Placentals are characterised by the possession of an allantoic placenta, a corpus callosum joining the two halves of the neopallium, and a typical dental formula of $i\frac{3}{3}$, $c\frac{1}{1}$, $p\frac{4}{4}$, $m\frac{3}{3}$. This number of teeth is, however, often modified and reduced.

At the beginning of the Eocene period there appeared a group of true Placentals which were primitive in that they were of small size, with tritubercular short-crowned molars, five fingers and toes, and walking on the flat of the hand and foot. Among them can be recognised some with a tendency to modification of the teeth for a carnivorous diet—the Creodonta, —others for a herbivorous diet—the Condylarthra. Others again were generalised Insectivora. Very early, a branch diverged from the Condylarthran stock and gave rise to the

Amblypoda, large, clumsy, premature rhinoceros-like forms such as Uintatherium, and which soon went extinct.

In the later Eocene divergent evolution has progressed, and it is very interesting to notice that a number of the Orders of Mammals have become differentiated, and that these are not yet split up into the various families. The Creodonta had given rise to the Carnivora, which branched out into the Pinnipedia or seals, and Fissipedia or dogs, cats, bears, civets, and badgers. The Rodentia came off from near the primitive Insectivora, as did also the Primates (Lemuroids and Tarsioids) and the Edentates. The Perissodactyla or odd-toed Ungulates emerged from a stock intermediate between Condylarthra and Insectivora, and blossomed out into the huge Titanotheres which soon went extinct, the horses, tapirs, and rhinoceroses. The even-toed Ungulates or Artiodactyla emerged from some form between the Creodonta and the Insectivora, and, apart from a number of short-lived groups, radiated out into the pigs and hippopotamuses on the one hand, and the camels, antelopes, deer, cattle, and giraffes on the other. Related to the Ungulates are the conies (Hyracoidea) and the elephants (Proboscidea). The whales (Cetacea) are regarded as having arisen from a stock related to the Creodonta, and the Sirenia may have a common descent with the Proboscidea. South America became inhabited by a peculiar collection of archaic forms which were all doomed to extinction, but of which some such as the Thoatheria had evolved into a very remarkable imitation of the horses. The Edentata include armadillos, sloths, and ant-eaters.

The Cheiroptera or bats are related to the Insectivora, while the Dermoptera have affinities with the Insectivora and Primates. In some cases sufficient fossil forms are known from successive strata to enable lines of descent to be traced with considerable precision. This applies especially to the horses, the camels, and the elephants. The evolution of the horses from Eohippus (Eocene) through Mesohippus (Oligocene), Miohippus (Miocene), Pliohippus (Pliocene) to Equus, was accompanied by a progressive increase in size, lengthening of the teeth which become " rootless," development of ridges

on the molars, fusion of ulna with radius and tibia with fibula, specialisation of the wrist and ankle joints into articulations allowing movement in only one plane, enlargement of the 3rd digit in hands and feet, and reduction of all the other digits until their disappearance.

The evolution of the camels from the Eocene Protylopus through Poëbrotherium (Oligocene), Procamelus (Miocene) to the present day is likewise a history of gradual increase in size, increase in length of the teeth and development of selenodont ridges on the molars, reduction of the upper incisors, enlargement of the 3rd and 4th digits in hands and feet with suppression of the remainder, and fusion of the 3rd and 4th metacarpals and metatarsals.

So far as is known the history of the elephants starts with the Eocene Moeritherium, of about the size of a pig, and with the primitive dental formula of $i\frac{3}{2}$, $c\frac{1}{0}$, $p\frac{3}{3}$, $m\frac{3}{3}$. Its ridged (lophodont) molars had only two ridges. In the upper Eocene, Palæomastodon was larger, and had a not inconsiderable trunk. The canines and all the incisors except one pair in each jaw had disappeared, and the molars had three ridges. Tetrabelodon from the Pliocene was still larger and its incisors were elongated into tusks, with persistent pulps. The molars had as many as six ridges and were so large that there was not room in the jaws for more than two teeth in each jaw on each side. Furthermore, instead of being replaced from beneath as in ordinary mammals, they were replaced from behind, the new tooth pushing the old one out forwards in front of it. It is worth noticing that although these animals grew large and tall, their necks were very short, and it is only by means of the long trunk that they were able to reach down to the ground for eating and drinking. The next step, shown by the Pliocene Mastodon, was accomplished by a shortening of the lower jaw and the loss of the lower incisor-tusks. Lastly in Elephas the grooves between the ridges on the molars become filled with cement. The ridges may be a dozen in number, and the maximum number of molars on each side in each jaw in use at one time is one and a half.

The history of the Primates is reserved for the next chapter.

LITERATURE

BROOM, R.   On the Origin of Mammals.   Philosophical Transactions of the Royal Society, Ser. B, vol. 206, 1914.

GREGORY, W. K., and SIMPSON, G. C.   Cretaceous Mammal Skulls from Mongolia.   Nature, vol. 118, 1926.

MATTHEW, W. D.   The Evolution of the Mammals in the Eocene.   Proceedings of the Zoological Society of London, 1927.

OSBORN, H. F.   The Age of Mammals.   Macmillan, New York, 1910.

WEBER, M.   Die Saügetiere.   Fischer, Jena, 1927.

THE EVOLUTION OF THE PRIMATES AND MAN

THE Primates originated from a stock related to the Insectivora probably in Cretaceous times. Plesiadapis, from the Early Eocene, had characters in common with the Insectivora and the Lemurs, which are the lowest Primates. The characteristic of the higher Primates is that the bony bar separating the orbit from the temporal fossa is complete ; or in other words, the eye-socket is round and protected all round by bone. At the same time, both eyes look more or less forwards so that their fields of vision overlap and may coincide (stereoscopic vision). There are five fingers and toes, and the first digits are opposable to the others, except in the case of the first toe of man. This opposability makes the limbs efficient grasping organs, and is evidence for the fact that the early Primates lived on the branches of trees. It will be seen in the sequel that this arboreal habit had consequences of the highest importance in the evolution of the Primates. Lastly, the most important character of all in the Primates is the great development of the neopallium in the cerebral hemispheres.

In the Eocene the fossil Notharctus is found, representing the earliest member of the group of the Lemuroidea. It was very generalised, for whereas the primitive dental formula in mammals is $i\frac{3}{3}, c\frac{1}{1}, p\frac{4}{4}, m\frac{3}{3}$, that of Notharctus was $i\frac{2}{2}, c\frac{1}{1}, p\frac{4}{4}, m\frac{3}{3}$. From forms of this type the Lemurs must have descended. The Lemurs alive to-day are nearly restricted to Madagascar, though a few occur in Africa, Ceylon, and Malay. They are fairly primitive animals, but show certain specialisations which rule them out from the main line of Primate evolution. Among these may be mentioned the peculiar procumbency of the incisors of the lower jaw, with which they comb their fur.

The tail of a Lemur is long but not prehensile, and its skull may be recognised by the fact that the cavity of the orbit can still communicate with that of the temporal fossa beneath the postorbital bar.

Another Eocene fossil allied to Notharctus is Tetonius, the earliest representative of the group Tarsioidea. Tetonius had an enlarged rounded brain-case and a small face. Its brain must have been relatively larger than in any other known Eocene animal. It also was not on the direct line of descent owing to specialisations such as the loss of the lower incisors, but a close relative of it must have been the ancestor of Tarsius which lives at the present day. In Tarsius the postorbital bar is splayed out and almost but not quite prevents communication between the orbit and the temporal fossa. It shows important advances in the structure of the brain, and of the external ear. In the fact that it has a discoidal placenta with a thickened trophoblast hollowed out into lacunæ filled with maternal blood, and in the fact that the mesoderm appears very early in the development of the embryo, Tarsius resembles the higher Primates and Man, and differs from the Lemuroidea.

In the true monkeys, apes and man, or Anthropoidea, the orbit is completely shut off from the temporal fossa. From some Tarsioid ancestor with affinities to Notharctus there diverged a branch which gave rise to the New World monkeys. These forms which are included in the group Platyrrhinæ have a broad internasal septum with the nostrils wide apart, and a tail which is usually prehensile. They show a considerable advance in the structure of the brain, and in the fact that their dental formula is reduced to $i\frac{2}{2}$, $c\frac{1}{1}$, $p\frac{3}{3}$, $m\frac{3}{3}$. At the same time they are definitely off the main line of Primate evolution because of the structure of the tympanic bone which forms a ring.

The Old World monkeys, apes and man, form the group Catarrhinæ, in which the internasal septum is narrow, the tympanic bone forms a tubular external ear, the tail when present is never prehensile, and the dental formula is reduced to $i\frac{2}{2}$, $c\frac{1}{1}$, $p\frac{2}{2}$, $m\frac{3}{3}$.

The Catarrhinæ must have emerged in the Eocene period from Tarsioid ancestors related to those which gave rise to the Platyrrhinæ. In the Oligocene, Parapithecus is found, and from forms related to it the ordinary monkeys or Cercopithecidæ must have been derived. These forms are again ruled out from the main line of Primate evolution by specialisations such as the development of two transverse ridges on the molars. At the same time, the Cercopithecidæ, which include the baboons and mandrills, show a great development of the brain, which must have undergone an evolution parallel to that which went on in the stock leading to the apes and man.

The main stem of the Primates leading to the anthropoid apes and man was represented in the Oligocene by the little Propliopithecus. The fact that it was small is important, for so many divergent branches became specialised in the direction of large size, and in the search for the ancestors of the apes and man, choice is limited to forms considerably smaller than those to which they might have given rise. The anthropoid apes have lost the tail, they show a tendency to walk erect, the mechanism of pronation and supination of the hand is perfected, and the brain is greatly enlarged and developed.

A descendant of Propliopithecus was the Pliocene form Pliopithecus, which itself was an ancestor of the gibbon (Hylobates), the smallest of the apes. Other lines of descent from forms like Propliopithecus led to the Orang, and to the chimpanzee and Gorilla, while the main stem culminated in the Hominidæ and man. The apes while having highly developed brains and retaining the power to oppose the first toe to the others, have not got brains large enough to enable them to do otherwise than remain brutes, relying on their strength and their long canines instead of on memory, skill, and the neopallium. There are some characters possessed by adult modern man which are present in the young but lost in the adult apes. An example of these is the absence of large brow-ridges in young apes and man.

The fossil record of the Hominidæ is not by any means as complete as would be desired, but there is already sufficient evidence to enable an outline to be given of the more important

changes and modifications which accompanied the evolution of modern man : Homo sapiens.

The Hominidæ include all the members of the human family and it must be noted that they differ from other Primates not so much in matters of kind as in matters of degree.   Essen-
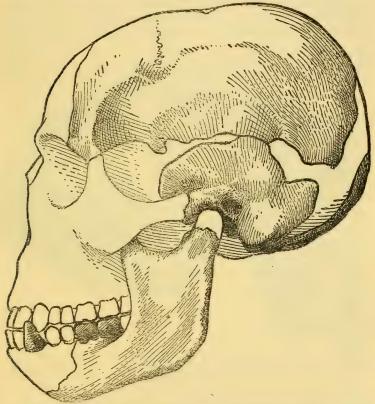
FIG. 180.—Professor John I. Hunter's reconstruction of the Piltdown skull, drawn by T. L. Poulton.   (From Elliot Smith.)

tially, the evolution of the Hominidæ is a story of enlargement of the brain, reduction of the nose, face, and jaws, perfection of the erect position, and loss of opposability of the large toe, which last feature converted the Quadrumana or apes into the Bimana or men.

The nearest approach to the human condition without achieving it on the part of an ape is Australopithecus, the Taungs skull, from South Africa. This fossil betrays kinship to the Gorilla and chimpanzee, but its brain is slightly larger and its face smaller.

The earliest known member of the human family is Pithecanthropus from Java. This form had a much enlarged brain with a cubic capacity of about 950 c.c., while the maximum
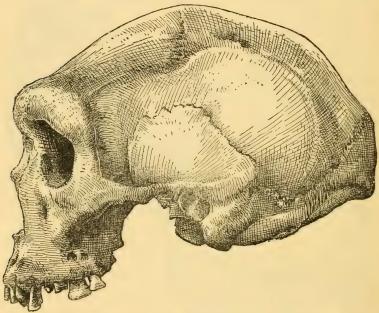
FIG. 181.—Skull of Homo rhodesiensis, drawn by T. L. Poulton. (From Elliott Smith.)

volume of an ape's brain is 650 c.c. From the structure of its femur, it walked almost erect. In some respects it preserves primitive features such as the continuity between the occipital and temporal crests on the skull, and many features in the conformation of the brain, but in others it is specialised, as in the development of the large brow-ridges.

The most important of all the human fossils is Eoanthropus, the Piltdown skull from Sussex. The bones of the skull are

very thick, and the lower jaw is strikingly similar to that of a chimpanzee, with no chin whatever, and large canine teeth. But the brain-case is dome-shaped and large, with a cubic capacity of about 1170 c.c., and there were no brow-ridges. The latter fact, together with the primitive nature of certain features in the brain, makes it possible to regard Eoanthropus as very close to the line of man's descent, if not his ancestor.

Pithecanthropus and Eoanthropus date from the latest Pliocene or earliest Pleistocene periods. The remaining fossil men come definitely within the period of the great Ice-Age.

The most primitive known member of the genus Homo is Homo rhodesiensis, from Broken Hill in Rhodesia. It had a brain-volume of about 1250 c.c., but still lacked any semblance of a forehead. There was no boundary between the nose and the face, and the palate was very big, but its chief specialisation is the development of enormous brow-ridges. The lower jaw is unknown, but it was probably not very different from that of Homo heidelbergensis from Heidelberg, which unfortunately is known only from the lower jaw. It is large and massive, without any chin. The teeth were definitely human, and primitive in that the last molars preserve five cusps, while those of modern man are often reduced to four.

Incomparably the best known of the fossil men is Homo neanderthalensis, specimens of which have been found from a number of localities in Europe, from Gibraltar to Palestine. In addition to the bones themselves, there is considerable evidence concerning these men from the weapons and tools which they fashioned from flint, and which consequently have been preserved. An indication of the degree of mental development of these people is obtained from the fact that some of the individuals which have been discovered appear to have been intentionally buried. The brain is very big (about 1350 c.c. on an average), but it preserves numerous primitive features. At the same time, the brow-ridges were large as were also the face, palate, and jaws. There was no chin, and the lower jaw preserves the large attachments for the digastric muscles. The vertebræ and the legs show that the neanderthal man

did not stand straight up, but stooped considerably. The hip-girdle was still long, and the foot rested mostly on its outer border, as in young children and certain savage races to-day. While having lost the capacity to be opposed to the other toes, the large toe was considerably separate from the remainder. The neanderthal race has gone extinct, doubtless because of its specialisations, and the insufficient development of the brain which handicapped it in the competition with Homo sapiens. Here, the brain has achieved maximum development, so much so that its front wall has been pushed forwards to form a more or less vertical forehead. This vertical wall of bone provides the necessary resistance for the reduced lower jaw to bite against. In the apes, Pithecanthropus, rhodesian and neanderthal man, where the lower jaw is still large and there is no forehead, the strain of the bite is taken up in the large brow-ridges which are developed in the adult. These brow-ridges are therefore not a primitive feature, but independently acquired as an adaptation in certain groups. Their presence, however, rules their possessors out from modern man's ancestry.

The face in Homo sapiens is relatively smaller than in any mammal, the lower jaw is slender and provided with a prominent chin, and the canine teeth are small. The hip-girdle is short and wide, and the vertebral column and legs enable man to stand bolt upright.

In connexion with the expansion of the brain and the assumption of an erect attitude, it is consistently found, on ascending the scale of Primate evolution to man, that the foramen magnum through which the spinal cord joins the brain is movedr elatively farther and farther forward. This fact is obvious when it is considered that the head of an ordinary lower mammal projects forwards horizontally from its neck, whereas man's head is carried vertically above his neck. At the same time, the eyes of lower mammals and of man look horizontally from about the middle of the front of the face. There has therefore been a progressive expansion of the hinder and upper part of the skull accompanying the development of the brain, and which moves the face-region farther and farther

forwards. The ordinary superposition of median vertical sections through skulls suffers from the fact that it is then difficult to distinguish between differences of actual size and differences of development. This difficulty vanishes when the sections are superposed on a common centre, and then rotated so that certain standard radius-lines coincide. Other lines

FIG. 182.—The skeletons of Neanderthal man and of modern man compared. (From Boule.)

can then be read-off by angular measurement regardless of the actual size of the skull. The centre of gravity is chosen as the common centre since it is the morphological centre of form. It may be called Sollas' centre. The sections are then rotated so that the radius-lines from the centre to the middle of the foramen magnum coincide. The sections are then " set," and reference-lines are made by continuing the radius of

coincidence up to the top of the skull, and drawing a line at right angles to it through Sollas' centre.

One of the most instructive readings is the measurement of the angle made between the line of the foramen magnum, and the line from the centre to the point of junction between the nasal and frontal bones (the nasion). It is essential for this comparison that the sections be taken from specimens of equivalent age, for during development the angle changes. Nevertheless, taking adult material it is possible to make out the following :—

Angle between foramen magnum and nasion in adult :

Gibbon	238°
Chimpanzee	239°
Pithecanthropus	251° (conjectural)
Homo neanderthalensis	253°
Homo rhodesiensis	262°
Eoanthropus	264° (conjectural)
Homo sapiens	circ. 270°

These measurements show that the periphery of the brain-case in modern man amounts to three right angles, and it is interesting to note in comparison with lower forms that the accommodation for the increased size of man's brain is obtained by the angular increase in the periphery of the brain-case as well as absolute increase in size.

It is also noticeable that Eoanthropus approaches nearer to sapiens than do neanderthalensis and rhodesiensis, which is an additional reason for including the former but excluding the latter from sapiens' ancestry.

As regards Australopithecus, the following table shows the comparison between it and juvenile specimens of other forms.

Angle between foramen magnum and nasion in young :—

Orang	243°
Chimpanzee	252°
Australopithecus	258°
Homo sapiens child	282°

It is clear, therefore, that the Taungs skull approaches the human condition in this respect, though still remaining similar to the Chimpanzee.

Having now reviewed the material on which all study of
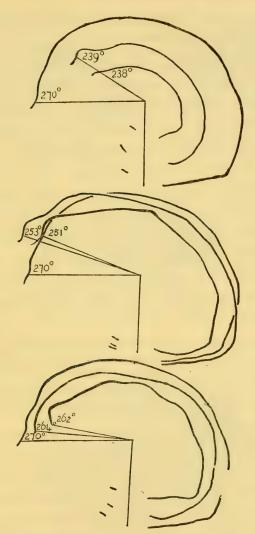
FIG. 183.—Diagrams of longitudinal sections of skulls, superimposed on their centres. (After Sollas.)

Showing the difference in angular measurement between the nasion-line (from the centre to the top of the nasal bone) and the line through the foramen magnum (from the centre) : in Gibbon 238° ; in Chimpanzee 239° ; in Pithecanthropus 251° ; in Neanderthal man 253° ; in Rhodesian man 62°2 ; in Piltdown man 264° ; and in modern man 270°.

the evolution of man must be based, it remains to consider what causes were probably operative during the history of human descent.   It may be said at once that just as the rise of the mammals was due to the development of the brain and formation of a neopallium, so a continuation and perfection of that process led to the rise of the Primates and man, and that this development was largely associated with the sense of sight.
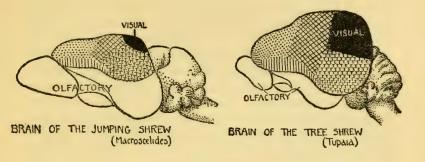
It has been seen that the history of the Primates can be traced from Insectivore-like ancestors, through Tarsioid, monkey, and ape stages, and that their evolution was accomplished under arboreal conditions of life.   Now, the Insectivora, Tarsioidea, monkeys and apes have living representatives at the present day, some of which have changed but little from their Eocene ancestors.   Without in the least suggesting that these living forms are on the main line of descent (which indeed it has been shown carefully that they are not), they may be taken and studied for their brains and organs of sight, as showing grades of structure approximately representative of the stages through which it is known that the Primates passed.
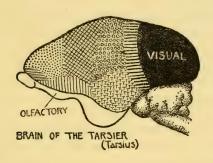
Of the Insectivora, Macroscelides (the jumping shrew) may be taken as a primitive mammal, in which the neopallium is developed, but the archipallium related to the sense of smell is still very large.   In particular it is important to notice that the region of the neopallium (parietal region) related to the sense of sight is small.

Tupaia (the tree shrew) is related to Macroscelides, and the difference which it shows in its brain is related to the habit of living in trees.   Life in trees is conducive to the better development of the sense of sight, for jumping from one branch to another, and inefficient perception of spatial relations would lead to disaster.   Accordingly, it is not surprising to find that the visual area of the neopallium of Tupaia is better developed than in Macroscelides, and that in the nature of its retina and other features connected with the eyes, Tupaia approaches the Lemurs.

The stage represented by Tarsius, which is also arboreal, is of great importance, for here for the first time the sense of
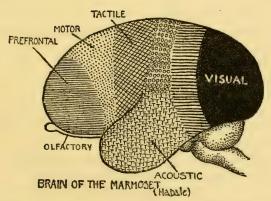
FIG. 184.—Diagrams showing the left side of the brains of Macroscelides, Tupaia, Tarsius and the Marmoset. (From Elliot Smith.)

Showing the increase in the area of the cortex associated with vision and co-ordinate movements (prefrontal), and the decrease in the olfactory region, in the evolution of Primates.

smell is reduced below the level of the sense of sight, which becomes the dominant sense in the body. The eyes of Tarsius look forwards, and the fact that they have rotated on to the front of the face necessitates the reduction of the nose and snout. At the same time, the senses of hearing and touch are better developed, together with their respective temporal and tactile areas in the neopallium. The development of the tactile area is important because it is associated with that area of the cerebral cortex which is concerned with the performance of delicately adjusted and skilful muscular movements. Such movements are essential for an active arboreal animal, but there is another reason for referring to this part of the neopallium, and that is that a portion of it (the prefrontal region) is concerned with the co-ordination of the movements of the two eyes.

In the prefrontal area of Marsupials there are centres which control the eye-muscles and therefore the movements of the eyeball of the opposite side. The movements of the two eyes are linked together in higher forms, and this is especially significant in the Primates, where the visual axes of the eyes become parallel. Further, whereas in lower vertebrates the fibres from each eye all go to the other side of the brain (the crossing at the optic chiasma is complete), in the mammals a certain number of fibres remain uncrossed, and go to the same side of the brain. Now, in the Platyrrhine stage of evolution, represented by the Marmoset, the co-ordination between the movements of the two eyes is perfected, and both eyes are able to follow one and the same object. A consequence of this is that " corresponding points " are developed in the retinæ of each eye, on which the images of one object are formed, and the most important of these points is the macula lutea or spot of optimum sensitiveness.

Consequent on the power of making conjugate eye-movements, the Anthropoidea have evolved a macula lutea, and this still further increases the importance of the parietal (visual) and prefrontal (skilled movement) areas, which features already distinguish the brain of the Platyrrhine from that of Tarsius. A continuation of the process of enlargement and perfection of the parietal, prefrontal, and temporal areas can be gradually

and serially traced through the Catarrhine, the ape (Gorilla), Australopithecus, Pithecanthropus, Eoanthropus, Homo rhodesiensis, Homo neanderthalensis to Homo sapiens. There is further the very interesting fact that in human development, the regions of the neopallium which are the last to be formed are precisely these parietal, prefrontal and temporal areas.

There is therefore good reason to believe that the perfection of these areas of the cerebral cortex and of the functions with which they are associated played the major part in the evolution of man. The brain developed first, and other features such as the reduction of the face and assumption of the erect attitude followed. It is to be noted that the perfection of the parietal and prefrontal areas is directly or indirectly concerned with the function of vision, so that it may be said that sight was of capital importance in the evolution of man. In this connexion, mention may be made of some other aspects of the bearing of sight on evolution.

In the first place, it will be remembered that the eyes are " distance-receptors," and that the responses which they evoke on the part of the animal are anticipatory rather than consummatory movements. Next, there is the fact that in man, the number of nerve-fibres entering the brain from one eye vastly exceeds the number of all the other afferent nerve-fibres of one side put together. From the physiological side, it is found that in the higher Primates including the monkeys, apes, and man, the eyes assume great importance in regulating the posture of the organism, a regulation which in lower forms is principally dependent on the semicircular canals of the ear. Lastly, from the psychological point of view, experiments on the behaviour of chimpanzees when confronted with problems shows that the eyes play a very important part in solving the problem. Cases of great interest are those in which there lies close at hand some instrument, such as a stick, and by using which the ape would be able to solve its problem easily. Unless the instrument to be used is seen by the ape in the same field of vision as the object or goal for which it is to be used, it pays no attention to it. Without this optic

co-presence, the ape does not " see " the solution to the problem.

Perhaps the most important of all the consequences of the perfection of the sense of sight in the Primates is the fact that it is the neopallium which undergoes commensurate development in the brain, and the neopallium is the physical companion of memory, of the ability to profit by experience, and of the arbitrator of possible responses, known as the will. There is also to be noticed here the importance of remaining unspecialised. For if the great development of the sense of sight had taken place earlier in evolution, in an ancestor of the mammals, it would have been not the neopallium, but the optic lobes which would have undergone specialisation, and for a number of reasons these are unsuited for the development of the higher mental faculties. The success of man is therefore also due to the fact that his ancestors did not shoot their bolt of specialisation prematurely.

A consequence of binocular vision and conjugate movement is the power to converge the eyes on an object. In the first place, this enables an estimate of distance to be made, which is important in leaping from branch to branch. Feeling of the degree of convergence is conveyed by stimuli from proprioceptive sense-organs in the eye-muscles by afferent fibres in the eye-muscle nerves. When, however, the eyes are converged on an object, that object occupies the attention of the animal, and the stereoscopic vision which it now enjoys enables it to become aware of the true geometrical and spatial relations of the objects in the world around it.

To return to the face, it is obvious that when the nose and snout are reduced as a result of the eyes coming on to the front of the face, the mouth itself can no longer so easily be used as a food-obtaining organ, as it is in lower forms. Here, the hands come to the rescue, and being five-fingered and with opposable thumbs, capable of pronation and supination, they undertake the function of carrying food to the mouth. At the same time, the development of the prefrontal area of the neopallium enables delicate movements to be made, in the course of which the animal acquires skill. It is an interesting

fact that in the higher Primates, the focal length of the eyes for most acute vision should be just within the reach of the hands. The assumption of the erect posture which is made possible by the increased power of co-ordination of the brain, relieves the hands from the service of locomotion, which is performed solely by the feet. The latter therefore lose the opposability of the big toe.

Lastly, in connexion with the greater development of the temporal region of the neopallium, the power of hearing became more acute, and with it came the development of speech. There is clinical evidence that in man, one of the lobes of the temporal region is concerned with the faculty of stringing words together into sentences with a logical meaning, and it has been shown above that this is one of the regions of the neopallium which has undergone progressive development in the evolution of man. It is not claimed that man is nothing more than a mammal which sees, hears, and co-ordinates his movements better than other mammals. All that is intended is to show that the development and perfection of these functions of sight, auditory discrimination with which must be coupled speech and language, and muscular skill, bring about changes which are prerequisite for the development of that peculiarly human attribute—the higher mental faculties.

LITERATURE

BOULE, M. Les Hommes fossiles. Masson, Paris, 1921. (English translation, Oliver & Boyd, Edinburgh, 1923.)

ELLIOT SMITH, G. Essays on the Evolution of Man. Oxford University Press, 1927.

GREGORY, W. K. The Origin and Evolution of the Human Dentition. Williams and Wilkins, Baltimore, 1922.

SOLLAS, W. J. Ancient Hunters. Macmillan, London, 1924.

SONNTAG, C. F. The Morphology and Evolution of the Apes and Man. John Bale, Sons and Danielsson, London, 1924.

THOMSON, A. A Consideration of the more Important Factors concerned in the Production of Man's Cranial Form. Journal of the Anthropological Institute. Vol. 33. 1903.

PART V

CHAPTER XLIII

CONCLUSIONS

Not the least of the interests aroused by the study of Vertebrates is due to the fact that they form a group which lends itself perhaps better than any to a consideration of general principles and matters of wide importance. This is largely because, although imperfect, present knowledge covers a considerable amount of the results of vertebrate evolution, and still more because between the most widely separated members of the group, between Amphioxus and man, there is sufficient similarity in plan of structure to enable comparisons to be made with advantage. Comparative Anatomy as an intellectual weapon is the more satisfactory when the number of correspondences of kind which can be established is great, regardless of course of matters of detail. So it is not astonishing that the Anatomy of, for example, Nematodes and Echinoderms when compared should be less fertile in conclusions of general interest than a comparison between Vertebrates as distant from one another as are fish and mammals. From the fact of the general homogeneity of the group as a whole, the variations to be observed in different vertebrates become all the more interesting.

It is very striking to find organs such as notochord, nerve-tube, dorsal and ventral nerve-roots, essentially the same in Amphioxus and man, but the most striking case of homologous organs is that of the thyroid. From the endostyle of Amphioxus, through Petromyzon with its tell-tale Ammocœte larva, to all the Craniates, the chain is complete, and not the

least remarkable feature of it is the great change in function which has taken place from an organ connected with the ciliary method of feeding to a ductless gland regulating the metabolism of the body. This case is a good illustration of the fact that function is no criterion whatever in questions of homology, and that the sole condition which organs must fulfil to be homologous is to be descended from one and the same representative in a common ancestor.

A fact which the vertebrates illustrate well, is that the numerical correspondence of segments which give rise to particular structures is not a necessary criterion for homology. This is well shown by a consideration of the pectoral and pelvic limbs. The fore limb is formed from trunk-segments 2, 3, 4, and 5 in the newt (Salamandra), whereas in the lizard it arises from segments 6, 7, 8, and 9. Similarly the hind limb arises from segments 16, 17, and 18 in the newt, but segments 26 to 31 in the lizard. Countless similar examples are afforded by other vertebrates, and it is to be noticed that the limbs not only vary in their position, but also in the number of segments which have contributed to their formation. Yet wherever they may be and however many or few segments they may contain, fore limbs are homologous throughout the vertebrates, and so are hind limbs. During evolution transposition has occurred ; new adjacent segments have taken to contributing to the formation of the limb, and at the opposite end segments which hitherto contributed may cease to do so. In this way the limbs may become transposed over the trunk of the animal much as a tune can be transposed over the keys. But it is the same tune and the same limb.

Another case is that of the position of the occipital arch at the back of the skull. The neurocranium of Scyllium occupies 7 segments while that of a form as closely related to it as Squalus occupies 9. Although they are situated in different segments, there can be no doubt that the occipital arches of these two animals are descended from the occipital arch of a common ancestor, and are therefore homologous.

A very interesting example of the same kind is furnished by the number of gill-slits in various Selachii. Heptanchus has

7, Hexanchus and Pliotrema have 6, and the remaining Selachi have 5 gill-slits and branchial arches on each side. Now the remarkable thing is that the last branchial arch has a typical structure whether it be the 7th, 6th, or 5th. Its peculiarity consists in the fact that its pharyngobranchial element is attached to that of the preceding arch, and it receives a portion of the trapezius muscle. The function of the last branchial arch is to anchor the branchial basket on to the shoulder-girdle. This being so, in the course of the evolution of forms with 5 branchial arches from forms in which there were 6,* it is impossible to imagine that the transformation took place gradually by reduction from behind ; for if this had occurred, there would have been stages in which the " old last branchial " arch had partly disappeared and the " new last branchial " arch had partially been modified to replace the former, and it is difficult to see how such an arrangement could have fulfilled the function of providing attachment between the branchial basket and the shoulder-girdle. This case is therefore different from that of the limbs, for in the latter there is nothing to prevent gradual transposition of the limb by means of partial modification of adjacent segments. Still less can it be imagined that the number of branchial arches has been altered by reduction from in front because the first two visceral arches, the mandibular and hyoid, are constant throughout the Gnathostomes. The only explanation left is that there has been a sudden change in evolution, and that a form with, say, 6 branchial arches gave rise to offspring with 5, without any intermediate stage of functional inefficiency. This conclusion is, of course, interesting from the point of view of evolution, but it is also not without importance as regards the relation of metameric segmentation to differentiation during development. The only difference between this hypothetical offspring with 5, and its parent with 6 branchial arches, is that the raw material for the production of the branchial arches has in the one case been divided up between 5 segments and in the other between 6 segments, during development. It is this raw material which is homologous in the two forms, regardless of the numerical

* Or *vice versa*.

position of the segment in which it is situated. A matter like this is worth some attention, for it is an example of how principles of general and wide interest can be derived from comparative anatomical studies.

In sharp contrast to homologous structures are the resemblances between different and unrelated groups of animals as regards characters which can be proved to have been separately and independently evolved. These resemblances are analogies, and they give rise to the phenomenon of convergence in evolution which is well illustrated by vertebrates. The instances of convergence which might be given are so numerous that only very few need be mentioned here. A good example is the modification of the pentadactyl limb into a paddle, thereby losing its typical appearance and presenting a superficial resemblance to the fins of fish. But the interesting thing is that this process has occurred not once but several times, independently, in different groups of Tetrapods : Chelonia, Ichthyosaurs, Plesiosaurs, Mosasaurs, Thalattosaurs, Thalattosuchia, Penguins, Cetacea (whales), Carnivora pinnipedia (seals), and Sirenia. The Ichthyosaurs and some of the Cetacea are further interesting in that they have developed median dorsal fins which are superficially very similar to those of fish. The Urodela also have median fins ; but in all these cases, a little study suffices to show that these structures not only differ very much from the fins of fish, but also that they differ between themselves.

Convergence is also to be found in the case of the elongated and limbless condition of Gymnophiona, certain lizards such as Anguis, Amphisbæna, Scincus, and the snakes. Or again, the fore limb has been modified into a wing independently in Pterosaurs, birds, and bats. The marsupial " mole " Notoryctes is very similar to the true placental moles (Talpa).

Now it is noteworthy that these cases of convergence are each of them related to a particular mode of life. So the paddle-like modification of the limbs is an adaptation to life in the water, just as wings are adapted to life in the air ; the limbless condition is a form of adaptation to a burrowing habit, while another form of this habit characterises the " moles." It is

because of their adaptations to their environment that these animals come to resemble one another, and these adaptations have of course no value in determining affinities or descent.

Another phenomenon may now be considered, which is in some ways intermediate between homology and convergence. It is often the case that in two groups of related animals which have recently diverged the same evolutionary changes take place. This may be called parallelism, and it is illustrated in certain groups of Ungulates such as the Titanotheres and the rhinoceroses. In several distinct stocks of Titanotheres peculiar bony knobs appear on the skull. These structures were not visibly present in the common ancestor of the forms which have evolved them ; the structures cannot therefore strictly be called homologous, yet they are so similar that it is impossible to avoid the impression that they have some common cause. The independent development of such similar structures in related groups of animals is often ascribed to a so-called process of " Orthogenesis," or variation along " straight " and constant lines. The working of this process in two or more related groups is supposed to result in parallel evolution.

Now it is worthy of note that when tracing lines of descent through fossil forms, it is rarely possible to identify one form as the direct ancestor of another. Instead, it is more usual to find that one fossil form is related to the ancestor of another, because it possesses characters which that ancestor must have possessed, while at the same time showing other characters which proclaim that it had diverged from that ancestor. The characters of the ancestor in question are, of course, to a certain extent deducible from those of the form descended from it.

The incompleteness of knowledge of the fossil record makes it difficult to find " fathers," but it supplies a number of " uncles." The question now is this : why do the " fathers " and " uncles " resemble one another ? Cynognathus itself is not the ancestor of the mammals, for in several respects it is too specialised, but it must have evolved parallel with the ancestor of the mammals or it would not possess so many similarities. In the same way it can be shown that the later

Stegocephalians, which were not on the line of descent of the reptiles, nevertheless show a number of changes in evolution which took place parallel to those which were going on in their " cousins " the reptiles.

The answer must be that the " fathers " and the " uncles " inherited something from the " grandfather " which determines the course of their evolution. This something need not, however, have been visible in the " grandfather," so that the " fathers " and the " uncles " in which the something does become visible appear to have evolved it independently. In these cases there appears what may be called a latent homology between the structures in question, and which accounts for the so-called " Orthogenesis." In any case, it is most important to avoid the impression that " Orthogenesis " implies a purposeful or directive force, or that evolution takes place in straight lines. Such impression is quickly dispelled by a consideration of the record of success and failure of the different groups of animals during evolution. If a directive force were responsible for evolution, it would seem to be peculiarly malicious, for most groups of animals have been " directed " to their doom by extinction.

An insight into what " Orthogenesis " really means is given by a study of the *relative* sizes of parts of animals to the whole animals, at different *absolute* sizes. It is found, for example, that the size of the antlers in Red deer is relatively larger in large animals than it is in small ones. That is to say, that the larger a Red deer grows, the relatively larger do its antlers become, on the average. These cases are susceptible of mathematical treatment, and it is found that the antlers not only grow faster than the body, but they grow faster at a constant rate, for the ratio of the growth-rates of antlers and body remains constant. Organs to which this principle applies are called heterogonic, and Heterogony is of wide occurrence in the horns and bony nobs of various groups of Ungulate mammals. Now just as the heterogonic organ is relatively smaller in small animals, it is found as a rule that in two species of one genus both of which possess this organ, the larger species will have the relatively larger heterogonic organ. So

the antlers of the little Muntjack are relatively smaller than those of the larger Red deer. There are of course exceptions and complications, but from the present point of view, the main thing to notice is that for an organ which shows heterogonic growth to appear at all, the animal's body must have reached a certain absolute size. Now as the different races of Titanotheres evolved, their size increased, in common with nearly all the groups of mammals. Independently, each of these races of Titanotheres developed bony knobs on the skull, and as the size-increase of the animals continued, the bony knobs became relatively larger still. The bony knobs are heterogonic organs, and their independent appearance in different races is not due to any directive force, but automatically to the increase in size of the body of the animal. This increase of body-size was probably due to random variation selected by natural selection in the direction of greater size because it is (up to a point) advantageous, and has survival value. From the common ancestor of the different races it is only necessary to assume that the capacity was inherited to produce bony knobs if and when a certain body-size is reached. On this view, therefore, " Orthogenesis " does not mean direct*ed* evolution, but merely direct*ional*. It also enables an explanation to be given for the cases of extinction of animals in which the size of the heterogonic organ (consequent on the large size of the body) had become so great as to reduce the animal's chances of survival. This applies to the Irish elk, which was a very large deer with relatively immense antlers.

Attention must now be paid to the terms " primitive " and " specialised," which were defined early in this book, and which have been consistently used throughout. In the first place, it is necessary to notice that their meaning is relative, so that it is possible to find an animal which is primitive when compared with one and specialised when compared with another animal. A specialised animal is one which is committed to a particular line and so has a restricted potency of evolution. As a rule, specialised animals are adapted to a particular mode of life, and this adaptation has entailed either the development or loss of certain structures which render the animals unfit to live

in any other environment but their own.   Once committed, they are committed for always, for in its broad lines evolution is irreversible.

Primitive animals, on the other hand, are not committed to any particularly restricted mode of life ; they do not have any delicate adaptations with the structural modifications which they involve, and they are, in a word, generalised.

It is from generalised ancestors that the main groups of animals have evolved, and as these groups radiated out they became specialised in their various ways.   Specialisation and evolutionary capacity are roughly inversely proportional.

The significance of primitiveness and specialisation is thus related to evolution.   Amphioxus is primitive because it possesses many characters which the early ancestral Chordates must have had.   But its specialised characters show that it was not itself that ancestor.   Amphioxus is with regard to the higher Chordates not a " father " but an " uncle."

It is worth noticing that the primitive arrangement of several structures was segmental, and that as evolution proceeded this simple scheme was departed from.   So the gonads of Amphioxus, myotomes of Amphioxus, kidney tubules of Myxine, ribs of Cotylosaurs and respiratory centres of Raia show that " a pair of each in each segment " was the primitive outfit, on which evolution has worked.

When man is considered in relation to his ancestors, a significant fact emerges.   Man is not adapted to any restricted mode of life at all ; instead he is fitted for almost all sorts of habits and circumstances ; he is generalised not specialised, and that is one of the secrets of his evolutionary success.   His ancestors must have been among the most primitive and generalised of the mammals ; they did not live on the capital of their evolutionary capacities and spend it in exchange for delicate adaptations, which, while perhaps allowing of " easier living," would have resulted in side-tracking the race into a rut or backwater of life.

Lastly, mention may be made of the material which the vertebrates supply for a consideration of what is often called the Law of Recapitulation.   It is not astonishing that a group

as broad and as well known as the vertebrates should provide several examples of embryos which seem to reflect something in the ancestral stages of the forms to which the embryos in question belong. As an example, the gill-slits (or rather gill-
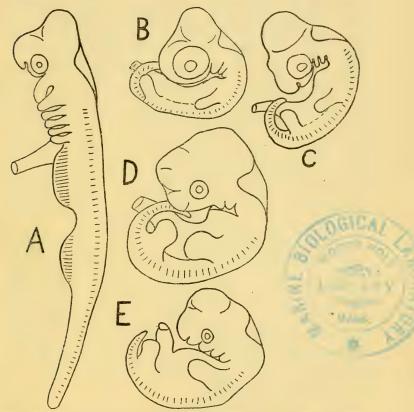
Fig. 185.—Views of embryos of A, dogfish ; B, lizard ; C, chick ; D, rabbit ; and E, man ; showing the similarity at early stages between embryonic forms of related animals.

pouches) of the mammals may be taken. It is rightly held that these structures in the embryo mammal represent the gill-pouches and slits of the fish-stage ancestor of the mammals. But the most important thing to notice is that it is the gill-pouches of *embryo* fish and not those of adult fish which the gill-

pouches of mammalian embryos resemble ; indeed, not much observation is needed to see that between the gill-pouches of the mammalian embryo and the gill-slits of an adult fish there is but little resemblance, whereas the gill-pouches of *embryonic* stages are very similar in all groups of vertebrates.   This explanation covers all cases of so-called recapitulation.   It follows that it is inaccurate and misleading to say that Ontogeny (the development of the individual) recapitulates Phylogeny (the evolution of the race).   What may be true is that Ontogeny recapitulates the *Ontogeny* of the ancestor, and even then, it is not necessarily true of all embryonic forms.   While the gill-pouches do recapitulate in this sense, other organs such as the primitive streak or the extra-embryonic cœlom do not.   It is also to be noted that the order of appearance of structures in Ontogeny is not necessarily the same as in Phylogeny.   Denticles appeared early in evolution, but they arise late in the development of the dogfish.   The embryo is phylogenetically older than the amnion, but in the development of the mouse, the amnion arises first and the embryo afterwards.

The real value of embryology from the point of view of evolution lies in the fact that embryonic forms are like the embryonic forms of related animals.   As a rule, the younger the embryos are, and the closer akin the species to which they belong, the more closely do the embryos resemble one another.   The more closely allied the species are, the longer does the resemblance between the embryos persist.   Embryology furnishes valuable evidence therefore as to affinities, but it cannot profess to give definite information concerning the *adult* forms of ancestors.

Literature

Bateson, W.   Problems of Genetics.   Yale University Press, 1913.

Garstang, W.   The Theory of Recapitulation : a Critical Restatement of the Biogenetic Law.   Journal Linnean Society, London, Zoology, vol. 35, 1922.

Goodrich, E. S.   Metameric Segmentation and Homology.   Quarterly Journal of Microscopical Science, vol. 59, 1913.

Huxley, J. S.   Constant Differential Growth-ratios and their Significance. Nature, vol. 114, December 20th, 1924.

Versluys, J.   Über die Rückbildung der Kiemenbogen bei den Selachii. Bijdragen tot de Dierkunde, vol. 22, 1922.

CLASSIFICATION OF THE ANIMALS AND GROUPS OF ANIMALS MENTIONED IN THIS BOOK

(An asterisk denotes a totally extinct group)

Phylum.	**Chordata.**
Subphylum.	**Hemichordata.**
Class.	**Pterobranchia,** *e.g.* Cephalodiscus.
Class.	**Enteropneusta,** *e.g.* Balanoglossus.
Subphylum.	**Protochordata (Acrania).**
Class.	**Urochordata.**
Order.	**Ascidiacea,** *e.g.* Ascidia.
Order.	**Thaliacea,** *e.g.* Salpa.
Order.	**Larvacea,** *e.g.* Fritillaria.
Class.	**Cephalochordata,** *e.g.* Amphioxus.
Subphylum.	**Craniata.**
Grade.	**Anamnia.**
Branch.	**Cyclostomata.**
Class.	**Cyclostomata.**
Subclass.	**Petromyzontia,** *e.g.* Petromyzon (? Palæospondylus).
Subclass.	**Myxinoidea,** *e.g.* Myxine, Bdellostoma.
Class.	**Ostracoderma,*** *e.g.* Cephalaspis.
Branch.	**Gnathostomata.**
Class.	**Pisces.**
Grade.	**Chondrichthyes.**
Order.	**Selachii,** *e.g.* Scyllium, Squalus, Heptanchus, Hexanchus, Heterodontus, Pristis, Rhina, Pliotrema, Raia, Torpedo.
Order.	**Holocephali,** *e.g.* Chimæra.
Order.	**Acanthodii,*** *e.g.* Acanthodes.
Order.	**Pleuracanthodii,*** *e.g.* Pleuracanthus
Order.	**Cladoselachii,*** *e.g.* Cladoselache.
Grade.	**Osteichthyes.**
Subclass.	**Teleostomi.**
Order.	**Osteolepidoti,*** *e.g.* Osteolepis, Sauripterus.
Order.	**Cœlacanthini,*** *e.g.* Undina.
Order.	**Polypterini,** *e.g.* Polypterus.
Order.	**Palæoniscoidei,*** *e.g.* Cheirolepis.

Order.	**Acipenseroidei**, *e.g.* Acipenser.
Order.	**Amioidea**, *e.g.* Amia.
Order.	**Lepidosteoidei**, *e.g.* Lepidosteus.
Order.	**Teleostei**, *e.g.* Gadus, Amiurus, Ipnops, Periophthalmus, Fierasfer, Gobiesox, Amblyopsis, Lucifuga, Solea, Exocœtus, Edriolychnus.
Subclass.	**Dipnoi**, *e.g.* Ceratodus, Lepidosiren, Protopterus, Dipterus.
Class.	**Amphibia.**
Order.	**Labyrinthodontia *** (Stegocephalia),
Suborder.	**Embolomeri**, *e.g.* Eogyrinus, Loxomma.
Order.	**Urodela**, *e.g.* Triton, Salamandra, Proteus, Siren.
Order.	**Anura**, *e.g.* Rana, Pipa, Rhinoderma, Alytes, Hylambates.
Order.	**Gymnophiona**, *e.g.* Ichthyophys, Hypogeophys.
Grade.	**Amniota.**
Class.	**Reptilia.**
Subdivision.	†**Cotylosauria,*** *e.g.* Seymouria.
Subdivision	**Sauropsida.**
Order.	†**Chelonia**, *e.g.* Testudo, Chelone, Sphargis, Eunotosaurus, Triassochelys.
Group.	**Parapsida.**
Superorder	**Squamata.**
Order.	**Lacertilia**, *e.g.* Lacerta, Varanus, Uromastix, Gecko, Anguis, Chalcides, Scincus, Amphisbæna, Chamæleo, Mosasaurus.
Order.	**Ophidia**, *e.g.* Vipera.
Superorder and Order.	**Ichthyosauria**, *e.g.* Mixosaurus, Ichthyosaurus, Ophthalmosaurus.
Group.	**Diapsida.**
Order.	**Rhynchocephalia**, *e.g.* Sphenodon (? Thalattosaurus).
Order.	**Crocodilia.**
Suborder.	**Pseudosuchia,*** *e.g.* Euparkeria.
Suborder.	**Thallatosuchia,*** *e.g.* Geosaurus.
Suborder.	**Eusuchia**, *e.g.* Crocodilus.

† The **Cotylosauria** and **Chelonia** are often grouped together as **Anapsida.**

Order.	**Dinosauria.***
Suborder.	**Saurischia,** *e.g.* Diplodocus, Tyrannosaurus.
Suborder.	**Predentata** (or **Ornithischia),** *e.g.* Iguanodon, Stegosaurus, Triceratops.
Order.	**Pterosauria,*** *e.g.* Pteranodon.
Subdivision.	**Theropsida.**
Group.	**Synapsida.**
Order.	**Theromorpha,*** *e.g.* Cynognathus.
Group.	**Synaptosauria.**
Order.	**Sauropterygia,*** *e.g.* Nothosaurus, Plesiosaurus.
Class.	**Aves.**
Grade.	**Archæornithes,*** *e.g.* Archæopteryx.
Grade.	**Neornithes.**
Subclass.	**Palæognathæ,** *e.g.* Struthio, Emu, Rhea, Cassowary, Apteryx (Kiwi), Moa, Tinamu.
Subclass.	**Neognathæ,** *e.g.* Columba, Gallus, Megapode, Grebe, Petrel, Diver, Gull, Flamingo, Duck, Phalarope, Dodo, Solitaire, Humming-bird, Penguin.
Class.	**Mammalia.**
Grade.	**Multituberculata.***
Grade and Subclass.	**Monotremata,** *e.g.* Ornithorhynchus, Echidna.
Grade.	**Ditremata.**
Subclass.	**Trituberculata.***
Subclass.	**Marsupialia,** *e.g.* Didelphys, Cœnolestes, Dasyurus, Thylacinus, Perameles, Phascolarctos, Phascolomys, Phalanger, Notoryctes, Thylacoleo, Macropus.
Subclass.	**Placentalia.**
Order.	**Deltatheridiidæ,*** *e.g.* Deltatheridium.
Order.	**Creodonta.***
Order.	**Carnivora.**
Suborder.	**Fissipedia,** *e.g* . Canis, Felis, Ursus, Civet, Badger.
Suborder.	**Pinnipedia,** *e.g.* Seal.
Order.	**Condylarthra.***
Order.	**Amblypoda,*** *e.g.* Uintatherium.
Order.	**Ungulata.**
Suborder.	**Perissodactyla.**
Family.	**Titanotheridæ,*** *e.g.* Titanotherium.

Family.	**Tapiridæ,** *e.g.* Tapir.
Family.	**Rhinocerotidæ,** *e.g.* Rhinocerus.
Family.	**Equidæ,** *e.g.* Eohippus, Mesohippus, Miohippus, Pliohippus, Equus.
Suborder.	**Artiodactyla.**
Tribe.	**Suina.**
Family.	**Suidæ,** *e.g.* Sus.
Family.	**Hippopotamidæ,** *e.g.* Hippopotamus.
Tribe.	**Tylopoda.**
Family.	**Camelidæ,** *e.g.* Protylopus, Poëbrotherium, Procamelus, Camelus.
Tribe.	**Pecora.**
Family.	**Giraffidæ,** *e.g.* Giraffe.
Family.	**Cervidæ,** *e.g.* Cervus, Reindeer, Muntjack, Irish Elk.
Family.	**Bovidæ,** *e.g.* Ox, Zebu, Sheep, Goat, Antelope, Antilocapridæ, *e.g.* Antilocapra.
Order.	**Hyracoidea,** *e.g.* Hyrax (coney).
Order.	**Proboscidea,** *e.g.* Mœritherium, Palæomastodon, Tetrabelodon, Elephas.
Order.	**Sirenia,** *e.g.* Manatus.
Order.	**Cetacea,** *e.g.* Whale, Dolphin, Porpoise.
Order.	**Litopterna,*** *e.g.* Thoatherium.
Order.	**Edentata,** *e.g.* Bradypus, Cholœpus, Armadilloe, Pangolin.
Order.	
Order.	**Rodentia,** *e.g.* Lepus, Mus, Squirrel, Porcupine.
Order.	**Insectivora,** *e.g.* Mole, Hedgehog, Shrew, Plesiadapis, Macroscelides, Tupaia.
Order.	**Cheiroptera,** *e.g.* Bat.
Order.	**Dermoptera.**
Order.	**Primates.**
Suborder.	**Lemuroidea,** *e.g.* Notharctus, Lemur.
Suborder.	**Tarsioidea,** *e.g.* Tetonius, Tarsius.
Suborder.	**Anthropoidea.**
Series.	**Platyrrhini,** *e.g.* Marmoset.
Series.	**Catarrhini.**
Family	**Parapithecidæ,*** *e.g.* Parapithecus.

Family.

Family.

Family.

Cercopithecidæ, *e.g.* Cercopithecus, Mandrill, Baboon.

Simiidæ, *e.g.* Propliopithecus, Pliopithecus, Hylobates, Simia (Orang), Chimpanzee, Gorilla, Australopithecus.

Hominidæ, *e.g.* Pithecanthropus, Eoanthropus.
Homo rhodesiensis,
Homo heidelbergensis,
Homo neanderthalensis,
Homo sapiens.

INDEX

References to generic names are in italics.

493